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REPORT OF INVESTIGATIONS — No. 91

AN ANNOTATED SYNOPSIS OF PALEOZOIC FOSSIL SPORES
AND
THE DEFINITION OF GENERIC GROUPS

BY
J. M. SCHOPF, L. R. WILSON, and RAY BENTALL

Prepared in collaboration with the Department of Geology,
Coe College, and the Tennessee State Division of Geology



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INTRODUCTION

The literature on fossil spores is scattered, and in addition there has been much diversity in methods of classification. The objects of the present article are to bring this material together in summary form for convenient taxonomic reference and to evaluate the genera which have been previously proposed. After a study of these microfossils in America and a thorough study of the literature it seems essential also to describe some new genera. It is hoped that a fundamentally sound basis has been provided for studies now in progress in the three laboratories represented by the authors and for future studies.

Guiding principles which relate to the treatment of this material are given below.

1. Only adherence to the systematic principles embodied in the International Rules will give satisfactory results in the study of these microfossils (as in other fields of paleontologic study). Therefore, the International Rules of Botanical Nomenclature, 3rd edition (Briquet), revised by the International Botanical Congress of Cambridge, 1930, and published in 1935,¹ have been used as a basis for taxonomic treatment.

2. Species classified within the same genus or under the same generic name must possess significant characteristics in common. There can be little positive proof of generic identity unless substantial homologous comparisons can be drawn between respective biocharacters of each congeneric species and the type species of the genus. For example many isolated lycopsid megaspores must be classified separately from the microspores found in

association with them because there is no adequate basis for close comparison of biocharacters exhibited by these diversified organs.

When affinities become better known so that the difficulty due to uncomparable features may be partially overcome, it then may be possible to relate the forms more naturally in classification within suprageneric groups such as tribe, family, and subfamily depending on how closely information may be correlated. Indeed, assignment to the same genus, or even species, is theoretically possible and may eventually be achieved in some few instances, but in general this implies a much more precise and detailed historical knowledge of interrelationships than is likely to be fully established.

For satisfactory nomenclature it is most convenient that those fossils which possess numerous demonstrably comparable features shall be placed under the same generic name. However, it is unsatisfactory to classify fossils under the same generic name simply because a few arbitrary features are held in common. The essential validity of any classification depends on the relative significance that attaches to the various biocharacters. In fact it is by virtue of such interpretive discrimination that taxonomy is to be distinguished from a cataloging procedure. Interpretations nevertheless must be based on evidence and not on supposition; difficulties are multiplied whenever interpretation exceeds factual bounds.

3. In paleobotanical practice there has been much divergence with regard to the significance and proper interpretation of unusually complete specimens in which parts usually found separated, and therefore generally classified separately, are

¹ Gustav Fischer, Jena.

found in organic union. Whatever attitude may be adopted, it is of fundamental importance for later consistent application of taxonomic principles. For this reason it seems desirable to state views applicable to the present work.

The few unusually complete specimens are highly significant in showing beyond question that certain isolated organs at a particular locality and stratigraphic level possess identity of relationship.* This identity must become more dubious, in the case of isolated parts, the further they are removed geographically and stratigraphically from the site of proved union. Stratigraphic discrepancy is most likely to cast doubt on specific identity; geographic discrepancy may be cause for qualification of the presumed relationship in varying degrees of subspecific magnitude (there is no basis for assuming that geographic races were less in evidence in the past than they are at present). If evolution is a more or less continuous attribute of life processes, over a period of time significant alterations in some of the many heritable characteristics are bound to occur. An individual alteration, although of specific significance, will not necessarily involve phenotypic expression in the majority of the other characteristics of the race. For this reason it is inaccurate to postulate the continued specific coordination of an extensive garniture of biocharacters over a period of time, without correspondingly detailed knowledge which proves that the characteristics dealt with were not subject to mutative or other evolutionary processes during that time interval. This detailed information is most readily determined for a restricted group of biocharacters which can be observed on common specimens. Practical reasons dictate that emphasis in systematic treatment be placed on the more common types of fossils rather than on those which show unusual preservation.

Demonstrated connections between spore forms and types of fructifications prove readily that some of the adjacent isolated specimens of either category are also conspecific. The diverse taxonomic groups, diagnosed on the basis of typical isolated specimens are proved, therefore,

to have coordinate significance through a part of their geologic life as species. During this particular period, identity of relationship must exist. But the most pertinent fact encountered in systematic treatment of the common isolated forms, is that this period of actual synonymy can scarcely ever be defined. As a general thing, due to discontinuity in the fossil record, it is impossible to establish the points at which old characters became coordinated in a new fashion or with other characteristics new to the phyletic succession.

Consequently these overlapping relationships do not lend themselves to taxonomic expression within specific and generic nomenclatural categories. Groups of suprageneric rank, which are less dependent on type specimens for their proper definition, may be better used in expressing such relationships of generalized validity. The present paper, however, does not deal with groups of suprageneric taxonomic status.

4. Various criteria for determination of synonymy have been used by paleobotanists. The practice we prefer is conservative to the extent that unless conspecific relationship is proved for two nomenclatural types, both names are valid. As such, they are available for any purpose of useful nomenclature. There are a large number of "partial synonyms" among the named species of fossil plants to which these remarks apply. The word "synonym" of course is an absolute term—"partial synonyms" are not synonyms; in most instances the names serve useful purposes in indicating groups of different circumscription. None of these names should be lightly considered; neither should a name be used in unqualified application unless its pertinence is evident. Evidences of "partial synonymy" undoubtedly record close natural relationship, but the names should not be regarded as invalid unless shown to be mutually inclusive. Lacking this, they remain applicable to fossils conspecific with their basic nomenclatural types. For the research worker there are advantages in this conservative view of synonymy, as it tends to promote a more precise differentiation of fossils. This basically, is a fundamental reason for the continued use of technical nomenclature, necessary to progress in the study of fossil plants.

* No plant, and certainly no single specimen, can have more than one valid name. However, instances arise in which it is difficult to determine which of two or more names should actually be applied. In spite of this, systematic procedure demands that an author follow some consistent usage.

5. Specific identification, because of its great significance, must be made critically. Emphasis should be placed on the positive evidence of similarity rather than on negative evidence of lack, real or fancied, of features which cannot be examined critically.

6. Neither spores, leaves, nor any other morphological part of a plant in any stage of its life is here considered to be a species. A species of plant, for the purposes of this synopsis, and regardless of how it may be otherwise defined, is regarded as a group of organisms. Any individual organism of such a group, however, may be identified if any diagnostic structure representing any portion of its life cycle is available. Spores in many instances are probably just as definitive of species as any other organ belonging in a coordinated manner to the life cycle of a particular plant individual. They merit study with other types of ancient plant materials, and all data should be recorded on a common basis of taxonomic equality. Because of their unique adaptation for dispersal and their numerical abundance in many sedimentary deposits, it is expected that spores will eventually become of greater practical significance than many of the larger types of plant fossils that are more commonly noted by the geologist.

7. Since the purpose of giving a name to a taxonomic group is not to indicate the characters or the history of the group, but is simply a convenience in reference, all names that are taxonomically valid and pertinent to recognized groups should be continued. The authors agree that the hyphenated generic nomenclature, for example, *Granulati-sporites*, *Laevigato-sporites*, *Denso-sporites*, instituted first by Ibrahim (1933), is in poor form, lacks euphony, and tends to be generally misleading. Nevertheless, the status of such names seems reasonably secure in several instances and their continuance is likely to cause less misapprehension than attempts to institute more appropriate nomenclature.

The preceding explanatory paragraphs may serve to clarify some of the policies adopted in this and subsequent reports and explain their consistency with systematic treatment of other types of plant material.

The earliest proposed name requiring

consideration is Dawson's *Sporangites*. This name was first proposed in 1863 and has been used ambiguously and in different senses by many authors. It is here regarded as a *nomen ambiguum* and the name *Tasmanites* is adopted for the most frequently encountered forms that have been commonly assigned to *Sporangites*. *Tasmanites* nevertheless is a problematic form, spore-like in many of its characteristics, but actually unassignable to any group of plants now known. All the other genera treated here belong with little doubt to the Cormophyta, and all whose affinity is approximately known belong to the Tracheophyte groups, as mentioned in the respective generic discussions.

Knox (1939, 1941) has suggested that spores of Bryophytes may be present in Carboniferous coals, and some forms that have been described may well belong to this group of plants which at present are very scantily recognized in the Carboniferous. The fact that no spores of Paleozoic Bryophytes are definitely known (*Sporogonites* Halle may be an exception) makes any suggested correlation hazardous at this time.

It is important to realize that many specific features of spores of different geologic age can be matched because of evolutionary convergence as well as because of community of derivation. Consequently unless there exists some corroborative evidence based upon spore forms actually present in contemporaneous fossils whose relationship can be established, all that seems warranted is to direct attention to similarity of the spores of different geologic age, recognizing that the similarities may or may not have phyletic implications.

There is some lack of strict agreement between the morphological nomenclature applied to modern pollen and the morphologic features of fossil forms. For one thing the microspore in modern forms is determined, in a strict sense, solely by the presence of the unicellular male gametophyte.² Such a distinction is of course inapplicable to fossil forms. There is also

² The common indiscriminate reference to all spores of relatively small dimensions as "microspores" is to be lamented. Although true microspores frequently are small, by no means all small spores are microspores. The long established botanical usage of the term "microspore" has reference to fundamentally functional distinctions that are entirely aside from relative or specific size. R. B. Thompson (1927) has in fact demonstrated that in some plants the microspore is larger than the actual megaspore.

the further difficulty that no simple correct morphological designation can be applied similarly to the dispersal forms of the male gametophyte bodies in both modern and fossil forms. The dispersal stage rather than the degree of gametophytic development is of greatest practical significance when fossils are considered. The terms perispore, exospore, and endospore might seem equivalent to the pollen structures perine, exine, and intine, respectively. However, in the case of the bladder-equipped fossil gymnospermic pollen, the bladder membrane which seems very similar in morphologic character to the perisporal membrane of certain cryptogamic forms, is regarded by many as equivalent to the exine of angiospermic pollen.

Revision of the morphologic terminology for fossil spores and similar microfossils also seems required. Not only has there been a dearth of descriptive terms available for description of the varied structural features, but a good many deeply rooted terms have become outmoded. Several of these date from the period in which *Selaginella* was presented as a primitive forerunner of modern seed plants, and their homologous implications now oftentimes seem unwarranted. Non-committal descriptive terms, which seem reasonably free of theoretical connotations, have been preferred for use in the present paper. It is hoped that it will be possible later to treat the descriptive morphology of spore forms specifically in greater detail.

In the synoptic lists the species assigned to each genus are given in alphabetical order. The order of genera adopted is chronologic according to the time each was first proposed. Although some intergeneric alliances can be recognized now, and a more logical sequence should be adopted in later works, it is felt that the chronologic order of priority will be of some convenience for taxonomic reference.

Nearly all the references cited (p. 62) are those of particular taxonomic or morphologic pertinence for the fossils discussed. Although we believe this represents a reasonably complete survey of this literature, it does not include all articles

that deal incidentally with Paleozoic spores. Various non-taxonomic systems have been used by some workers in designating types of spores in coal thin-sections, notably by Slater and his colleagues in the South Yorkshire laboratory of the British Fuel Research Division, by Th. Lang in Silesia and, most importantly, by Reinhardt Thiessen. These apply very slightly to the present work because species cannot be as reliably distinguished from spores in thin-sections, the significant biological characters are generally more difficult to ascertain, and the informal nomenclature used does not require systematic consideration. Consequently articles of this nature are not considered except in connection with the morphology of certain forms.

On the other hand, there is a considerable literature on isolated spores in the Russian language which needs to be given careful study before nomenclatorial stability can justifiably be hoped for. Thus far only a small portion of this literature has been available to us, chiefly in abstract form, and this is insufficient to provide a satisfactory basis for understanding the quite different nomenclature Russian writers have used. Naumova (1937) mentions that about 400 species have been distinguished based on material ranging in age from the Lower Carboniferous to Tertiary. He mentions genera designated as *Zonotriletes* and *Azonotriletes*. Nikitin (1934) has distinguished the genus *Kryshtofovichia* based on very singular appearing, large spores of Devonian age. Luber (1938) mentions subgroups (genera?) *Azonotriletes*, *Zonotriletes*, *Azonomonoletes*, *Azonaletes* and *Zonaletes* and distinguishes several apparently valid species. In a more recent publication Luber (1939) uses the generic (?) names *Plagilites*, *Turriella*, *Circelliella*, *Saccrimalia*, *Circella*, *Libumella*, *Spinosella*, *Subsacculifer* and *Plicatella*. It is to be hoped that under more favorable circumstances it will be possible to give full consideration to the Russian studies which have already been put to good use in the age determination and correlation of the widely separated coal deposits of the USSR and to integrate the nomenclature they are using with our own.

GENERA OF FOSSIL SPORES

Genus TASMANITES Newton, 1875

Sporangites Dawson, 1863 (pars.), Canadian Naturalist, New Ser. vol. 8, no. 6, pp. 431-457.

Plate 1, figure 1

General Discussion.—There is a group of highly distinctive fossil spore-like bodies which occur most notably in the Devonian-Mississippian black shale that requires a name amenable to standard taxonomic usages. At first, it was supposed that the name *Sporangites*, if supported by an emended definition, could apply. We are now of the opinion that the application of that name is not correct in this connection, and that the various descriptions that have appeared for *Sporangites* are so highly conflicting and ambiguous or erroneous that that particular name should be considered a *nomen ambiguum*. This is herewith proposed in view of the difficult taxonomic situation as detailed below.

The present most common use of the term "*Sporangites*" is by geologists who wish to record the presence of more or less disc-shaped, resinous-appearing bodies that are very commonly found in the Devonian-Mississippian black shale, many, but by no means all, of which are properly referable to *Tasmanites* as given below. This common usage does not conform to the original application of the name and is so noncritical and general in application that it would probably be unwise to attempt to restrict it even if this could be done in accordance with taxonomic procedure. Possibly no one, certainly not its author, has used the term with taxonomic consistency and practically all records of *Sporangites* must merely be regarded as indicative of some small rounded, brownish or yellowish bodies. Needless to say, many kinds of plant microfossils correspond to this characterization. However, there is no reason why "*sporangites*" may not be continued to be used in this sense, since it serves a descriptive purpose, in spite of the fact that it is botanically misleading; but the name should not be italicized or treated as a generic designation.

Sporangites was first proposed by Dawson in 1863 (p. 454). Here he

applied the name to spores or "spore cases" which he thought were referable to *Lepidodendron*, *Calamites* and similar plants. *Sporangites papillata*, about one inch (!) in diameter, and *S. glabra* about the size of a mustard seed, were mentioned; later this description was repeated, accompanied by small diagrams (Dawson, 1865, p. 165, pl. 12, figs. 80-81). These fossils were associated with coal at Joggins, Nova Scotia, and may in part have been material that would be placed now with *Triletes*, but there is no way to confirm this from his description or illustrations. His repeated descriptions of *S. papillata* as "one inch in diameter" leads one to suspect it may have been a seed. In 1871 (a, b) Dawson described an additional species from the black shale at Kettle Point on Lake Huron as *S. huronensis*; "small globular papillate spore-cases—probably of some *Lepidodendroid* plant." Later in the same year (Dawson, 1871c) he also referred a specimen consisting of a small whorl of leaves or bracts, first described as *Annularia acuminata*, to *Sporangites*. This last interpretation of *Sporangites* was accepted by Stopes (1914). Forms similar, in general, to those from Kettle Point are usually construed as *Sporangites* by present day geologists, but it seems evident that neither of these interpretations corresponds at all closely with Dawson's first generic application of the name.

Dawson in 1883 presented a report on "Rhizocarps in the Paleozoic Period" at the meeting of the American Association in Minneapolis, an abstract of which appeared in the American Association for the Advancement of Science proceedings (1884a). The entire paper also appeared in the Canadian Record of Science for the same year (1884b). The essential descriptive part and the figures are identical in both. Here Dawson proposed the name *Protosalvinia* including two species given as "*Sporangites (Protosalvinia) brasiliensis* n.s.," and "*S. (P.) bilobatus* n.s." Dawson stated that if we compare the separate macrospores of the Brazilian sporocarps, and especially those which are found detached from their envelopes (Sic!) with *Sporangites huronensis*, we

see a remarkable similarity in size, form and texture, sufficient to justify us in supposing that the latter may be of the same nature as the former, but deprived of their outer cases either by dehiscence or decay, and this is the view which we are now disposed to take of their nature. This better accords with their wide distribution in aqueous deposits and with their accompaniment than any other supposition. Plausible and satisfactory as this supposition may be, there is nevertheless scant basis for assuming *all* the various sporangite bodies to have such an origin, not to mention the insidiousness of attempting to apply scientific nomenclature on the basis of such a supposition. It cannot be said that Dawson ever proved the identity of bodies within and outside the "sporocarps"; furthermore, no one else has ever provided any conclusive evidence. Evidently many have taken this important point for granted, however, because the two names are used practically interchangeably in much of the subsequent literature.

The "spherical and oval sacs, the walls of which are composed of a tissue of hexagonal cells . . . ; three to six millimeters in diameter," apparently are properly assignable to *Protosalvinia* Dawson, 1884. We are unable to ascertain their characteristics reliably from any figures Dawson published but White and Stadnichenko (1923) give photographs and data on a form, *Protosalvinia ravenna* White, 1923, which is confirmatory of their thalloid characteristics, although White regarded them as sporangia. White (p. 239) has repeated the suggestion, (which seems to have originated with Dawson, 1871a, b) that their affinity was probably with "Devonian types antecedent to the Carboniferous Lepidodendra and Sigillariae." Possibly he thought the sporangite bodies were actually spores of lycopod relationship, as many others have, and he probably accepted their supposed relationship with *Protosalvinia* because of close association. Oval specimens of *Protosalvinia* bear some resemblance to lycopod sporangia, but there are general objections to such an interpretation. Even when they are occasionally in abundance no cones or actual lycopodiaceous remains are noted in the same assemblage (Dawson reported some du-

bious lycopod stem material, but no thalli or "sporangia" with the "spores" at Kettle Point). White seems to have made no close study of the sporangite forms under appropriate magnification and he found none of them actually in any of the multitudinous "spore cases" (thalli?) of *Protosalvinia* which were examined. In fact, although an uncritical reader may infer from this work that "*Sporangites*" belongs to *Protosalvinia*, White actually made no direct statement to this effect and he possibly had no strong convictions as to their nature. As the association of thalloid bodies with sporangite forms is by no means common and as the sporangites that have been reported differ considerably (one of the generic types here being treated as *Tasmanites*), it is evident that *Protosalvinia* and *Sporangites* cannot be in any way accurately treated as synonyms. No one yet has furnished tangible evidence of the nature of the spore-like bodies Dawson reported actually within the *Protosalvinia* thalli, so it still is quite speculative whether any relationship (other than that of a common environment) is evidenced by their infrequent association in the Devonian-Mississippian black shale.

Dawson reviewed the subject in connection with his paper in the bulletin of the Chicago Academy of Science in 1886 (pp. 105-118), calling attention to Orton's (1882) discovery of *S. huronensis*-like bodies in the Ohio shale, Clark's (1885) description of somewhat similar material in the Devonian of New York, the report of Johnson and Thomas (1884) on these microscopic discs in the Chicago water supply and glacial till of the region, Newton's (1875) description of *Tasmanites punctatus*, and his own (Dawson, 1884a, b) descriptions of two lots of Brazilian material sent him by Hartt and by Orville Derby. He makes no direct mention either of the Joggins specimens or of "*Sporangites*" *acuminata*. This article is the best of any written by Dawson on the subject. Nevertheless, in it, as well as in his other papers, the inadequacies of his concepts are fully apparent. He appears confused as to the distinction between spores and sporangia; he definitely considers the *S. huronensis* bodies referable to the water ferns (hence, *Protosalvinia*), being misled on the one hand by the fal-

lacious idea of the primitiveness of that group of living plants, current at the time, and on the other by association with the (probably unrelated) thalloid plants sometimes found in the same beds. Dawson considered his study of the Brazilian material particularly conclusive but his account of it does not seem so now and, unless the original material can be re-studied or new material obtained, the specific nature of the Brazilian specimens is entirely problematic.

Jongmans more recently (1930) has listed most of the nomenclature rather indiscriminately under the name *Protosalvinia*. His treatment is hard to comprehend inasmuch as *Sporangites* and *Tasmanites* are treated as synonyms although their precedent publication dates are given with approximate correctness.³ In attempting to follow Dawson's somewhat confused usage and apply it more widely without original study, Jongmans has not contributed to the understanding of these plants or lessened the confusion in nomenclature. His omission of some pertinent references may in part be responsible for the rather misleading impression conveyed by this portion of the Catalogus.

One other thalloid plant occurs in association with sporangite forms in the black shale which now can be more adequately discussed because of reexamination by modern methods. Spores are present in it and are quite different from sporangite bodies, in spite of Dawson's suggestion that they were similar. Dawson (1888) called this form *Sporocarpum furcatum*. In the most thorough and essentially definitive study of this plant by Kidston and Lang (1925), Dawson's name was continued. However, White, in White and Stadnichenko (1923), had renamed the group *Foerstia* but without taxonomic comment or discussion. Nevertheless the reason and justification for this new generic name is evident upon consideration of the genus *Sporocarpum* Williamson (1879, cf. also 1880, p. 509) which was founded upon *S. cellulosum* and similar forms of problematic affinity but quite

definite morphologic character. Many have considered the *Sporocarpum* types to be lycopod megaspores but from our present knowledge such a view seems untenable. Their structure is more reminiscent of colonial habit seen in the Volvocales. At any rate, there is no similarity between them and *Sporocarpum furcatum* Dawson. The name for this form must be *Foerstia furcata* (Dawson) Pia; Pia (1927) having been first to use this combination, but also without comment. The type species of *Foerstia* is best taken to be *Foerstia ohioensis* White, instead of Dawson's species. Kidston and Lang's work suggests that they may be specifically inseparable and if this is ever proved by comparison of the holotypes of the two species, White's specific designation, *F. ohioensis*, of course would become a synonym.

The spores of *Foerstia* occur in tetrads, to some extent localized along one margin within the fertile tips. Possibly they were formed in individual conceptacles. An analogy in more than one particular is suggested by *Fucus*, but aside from the possibility that *Foerstia* may also be an advanced type of alga, probably no interpretation of homology can be supported. The individual spores of *Foerstia* are about 200 microns in diameter, similar to those of land plants, with a heavy "resistant" spore coat about 7 microns thick, definite haptotypic structures consisting of trilete sutures with pyramidal areas well defined by distinct arcuate ridges. The distal part of the spore coat is irregularly pitted and somewhat rugose according to information presented by Kidston and Lang. Thus, these spores are entirely different from the sporangite bodies that may be associated with them.

Haptotypic features have been described for the spores in all reliable reports that have ever been published of bona fide Devonian plants showing these reproductive structures. These spore forms, in addition to *Tasmanites* and its associates, may be found isolated in carbonaceous Devonian sediments. Lang (1925) has shown that eight or more distinct species are thus represented in the Cromarty fish-beds of Old Red Sandstone age in Scotland. None of these can be referred to *Tasmanites*, although Lang's spore-type F (in part), which

³ Dawson's paper in the Canadian Naturalist for 1870 evidently appeared subsequent to publication of his paper in the Am. Jour.; Sci. for April, 1871. The paper "On Rhizocarps, etc." published in the Canadian Record of Science is dated and evidently was published in 1884, rather than 1885. Such minor errors are unfortunate in a reference so widely used as the Fossilium Catalogus.

seems to lack haptotypic features, may be generically similar to some of the spore-like rugulose-membranous associates of *Tasmanites* in American deposits. So far as these plant microfossils and others of similar character but questionable nature are concerned, an adequate study of them is hardly begun.

The essential point to be made in regard to "*Sporangites*," which geologists generally consider is well known, is that Dawson applied the name in the first place to ambiguous material and then later applied it without consistency to specimens of at least two other diverse and unrelated types. He further confused its application in conjunction with at least two other generic names. Geologists have accepted one of the usages of Dawson, but as this does not correspond with Dawson's original interpretation it seems impossible to retain it in systematic usage. The term "sporangite" ought therefore to be considered no more than a descriptive designation without taxonomic implication.

The systemic designation *Tasmanites* was rejected by Dawson who recognized the similarity of *Tasmanites punctatus* Newton (1875) to his *Sporangites huronensis* (Dawson 1886, p. 116) because, as the "name *Sporangites* had priority, I (i.e., Dawson) do not think it necessary to adopt this term (*Tasmanites*), although there can be little doubt that these organisms are of similar character." This similarity can be verified from Newton's illustrations by any one who has carefully examined abundant sporangite specimens from the Devonian-Mississippian black shale, but the similarity is by no means evident if all the various inadequate figures of "*S. huronensis*" given by Dawson and his contemporaries are consulted.

The best evidence that at least many of Dawson's *S. huronensis* specimens, and particularly those expressly mentioned by Orton, are similar to those of Newton has been presented in the creditably illustrated work by P. F. Reinsch, vol. II of the *Micro-Paleophytologia*, published in 1884. Material from the Ohio shale and from Chicago sent by Orton and B. W. Thomas is described and illustrated and comparisons are readily made with similar material from

Newton's tasmanite which Reinsch obtained from the British Museum. Reinsch assigned these forms, along with others, in his group called the Discieae, characterizing them generally as

compressed disc-like plant bodies of original subspherical or subelliptical outline. They are entirely closed, with walls sometimes perforate and show a thin central cavity which has been reduced by compression.

Variations in the walls are mentioned due to inclusion of other forms which seem to resemble *Calcsphaera* Williamson (1880, p. 521), *Sporocarpion* Williamson (1879, pp. 346-349; 1880, pp. 507-11), and many other diverse forms, some of which may even represent true sporangia of articulate plants. Reinsch also described 15 kinds of Discieae from the older Mesozoic. For the most part forms derived from the Carboniferous of central Russia and Saxony contrast sharply with the *Tasmanites* forms from America, Australia and Tasmania. These last evidently were chiefly in mind as he described the Discieae, for his group description fits them best. Specific nomenclature is applied to only one form so that Reinsch's work, although it shows best the characteristics of various *Tasmanites* specimens, is essentially not a taxonomic contribution. But since it establishes the similarity of American and Tasmanian forms we may feel no hesitancy in calling these peculiar bodies *Tasmanites* and in accepting Newton's species as the type for the genus. It seems so generally similar to some of the material provided by Orton and Thomas there is a question as to proper specific distinction between them, but being so widely separated geographically as they are, and stratigraphically as they seem to be, the forms should remain under separate names, at least until a definite first-hand study can be made. No specific definitions are attempted here, but it is felt that the generic definition given below is sufficiently accurate to serve to distinguish the group from forms which unmistakably are spores of cryptogams and higher plants, and from several other kinds of problematic fossils which are found in Illinois (and probably elsewhere) associated with *Tasmanites*, but which must be considered generically distinct from it.

Diagnosis.—An adequate description of *Tasmanites punctatus*, taken here as the type species of the genus, is given by Newton and excerpts from his paper (pp. 339, 340, 341) are quoted below:

When the separated discs are viewed by reflected light, they appear as more or less circular bodies, somewhat thickened towards the circumference, many of them having their surfaces raised into irregular folds. If mounted in canada balsam, and viewed by transmitted light, many have the appearance represented in pl. 10, figs. 2, 3, 8, while others exhibit the folds to which allusion has just been made. The more perfect discs are seen to be surrounded by a double contour-line—the optical expression of the fact that these discs are really thick-walled sacs. The saccular character, however, is best seen in transverse sections (figs. 1, 4, 5), or when the sac is broken (fig. 8). A closer examination enables one to see that the walls of these sacs are not homogeneous. A view such as fig. 8 shows numerous dots scattered over the surface, which become somewhat elongated towards the edges of the disc. When examined with a power of about 250 diameters, the dots can be resolved into minute circles about 1/3000 of an inch in diameter with a still smaller dot in the centre, as shown in fig. 9. These structures are best seen in the discs of White Coal. It may be thought that these dots are comparable to the granules to be seen upon the surface of some of the macrospores of *Flemingites*; but the study of transverse sections shows at once that these dots are not mere surface markings, for they can be distinctly traced as minute lines (tubes?) passing from the outer to the inner surface. These lines are shown in fig. 5, but owing to the section not being quite in the same plane as the lines, they do not appear to extend quite through. In addition to the fine lines, the walls of the sacs exhibit obscure longitudinal markings, which give them a laminated appearance (fig. 5).

Neither Mr. Carruthers (Geol. Mag. 1865, p. 432), nor Mr. MacNaughton (Trans. Roy. Soc. Van Dieman's Land, vol. ii, 1855, p. 116), mentions any structure in the walls of these sacs.

The discs vary in diameter, as stated by both these authors, from about 1/80 to 1/50⁴ of an inch. Mr. MacNaughton speaks of a thin outer coat to these discs, which may be seen when they are ruptured. I have examined all my preparations, both sections and separated discs, in order to distinguish this outer coat, but have been unable to do so. One easily recognizes in transverse sections, such as fig. 1, that the walls of the sacs vary much as regards thickness; and among the separated sacs which are mounted in balsam some may be seen much more transparent than the rest; but I have failed to see any real difference between the

⁴ 1/80 and 1/50 of an inch = 317.5 and 508 microns respectively. However, Newton's figure 2 "a large spore" given at 50x would be over 650 microns in diameter. From his figure 5 (250x) the wall is about 25 microns thick. In this specimen the wall is about 1/26 of the total diameter.

thicker and the thinner sacs, or to find them in anything like the relation of an inner and outer coat.

. . . . Prof. Balfour, I believe, considers the Tasmanite discs to be closely allied to *Flemingites*; they differ from them, however, as Mr. Carruthers has pointed out (Geol. Mag. 1865), both in structure and size. All the *Flemingites* macrospores which I have seen have homogeneous walls, and in many of them is seen the triradiate marking, which is so generally present in cryptogamic spores (Prof. Williamson, MacMillan's Mag., March, 1874, p. 409). In none of the Tasmanite sacs have I been able to see this triradiate marking, although their structures are so clearly shown that these markings could not fail to be seen if they were present; and the walls, as we have already seen, have a definite structure.

. . . . The inconvenience of having an object without a distinctive name induces me to propose one for the spores (?) found in Tasmanite and Australian White Coal (the two being, as I believe, identical in structure); and in order to retain existing titles as far as possible, I would suggest that Prof. Church's name *Tasmanite*, which is so generally used in reference to the schist as a whole, be retained for this substance, and that the spores (or rather the plant to which they belong) should be called *Tasmanites*, with the specific title of *punctatus*, in allusion to their surface-markings.

The features which are here regarded as generically characteristic of *Tasmanites* are as follows:

Symmetry.—Unicentric; there is evidently a center and not an axis of symmetry as in spores of bonafide plants.

Shape.—Originally spherical; except where protected, compression has altered them into disks with a few sporadic rounded folds.

Size.—Ranging from less than 100 microns to 600 microns or slightly greater diameter. Forms greatly in excess or much smaller than these dimensions are suspect, because they vary so greatly from the genotype species.

Ornamentation.—Surface smooth and glistening in reflected light at low magnification; more detailed examination shows more or less rugosity which may be in part attributable to preservation. More or less regularly spaced punctae varying in number on different forms are visible, but not conspicuous. The forms may be described as essentially lacking in external ornamentation.

Haptotypic features.—Entirely absent. False conclusions have been drawn either from different forms in association with *Tasmanites* or from specimens poorly

preserved and misinterpreted. Absence of trilete sutures is diagnostic.

Wall.—Generally moderately thick, mostly 1/10 to 1/25 of the diameter; wall evenly developed on all surfaces and never membranous, often punctate with pores tapering from very small orifice on the outside; sometimes the punctae are very sparse, in other species they may be so densely packed as to give a radially striate appearance. Poorly defined concentric bands may be present in the wall, but these are ordinarily not easily visible unless material is sectioned. In optical section (transmitted light) aside from the punctae, walls generally appear homogeneous.

Affinity.—The question of the affinity of *Tasmanites*, so far as it can be definitely discussed now, hinges on whether these bodies can be taken to represent plant spores or not. Spores of all plants above the algal stage that are readily preserved as fossils have markings on the spore coats of various but definite significance. All plant spores arise normally as tetrads (groups of four) from a single spore mother cell. All primitive plants (aside from algae) show evidences of their tetradic derivation in the structure of the spore coat. The *Tasmanites* forms do not show any such structure and, in addition, have fundamentally a unicentric symmetry which is in strong contrast to plant spores which are always radially or bilaterally symmetrical. Therefore, it seems conclusive that *Tasmanites* is not allied with any of the known primitive land plants. It may represent an algal type but if so, no correlative vegetative algal remains can yet be recognized.

The preceding remarks indicate that the writers' observations are by no means in agreement with Thiessen's (1921, 1925) on what, it appears, must include the same types of material. Thiessen persists in describing all forms from the black shale as if they had "tetrasporic" marks (in some cases more or less removed by abrasion). He definitely identifies them with Dawson's *Sporangites huronensis* and with the *Tasmanites* forms illustrated in 1884 by Johnson and Thomas (cf. Thiessen, 1921, p. 293) but discrepancies make it impossible to entirely confirm the statement. For ex-

ample, the form shown on his plate 10, figure A (1921) is stated in the text to be 0.85 mm. (850 microns) in diameter but the legend says it is magnified 140 \times , and measurement of the figure shows the form to be at that rate about 170 microns in diameter. It may be this form is the same as some observed in association with *Tasmanites* in Illinois, but should not be generically identified with it. The walls are generally quite rugulose-undulant and may show a poorly defined very coarse reticulation net, but the membranous character of the fossil suggests that it originally was smoother and that it has been impressed irregularly by grains of the enclosing sediments. No trilete suture (tetrasporic marking) can be demonstrated on material examined at first hand nor is any structure of this sort discernible in Thiessen's figures. Just as Newton remarked in his description of *Tasmanites punctatus*,

in none of the sacs have I been able to see this triradiate marking, although their structures are so clearly shown that these markings could not fail to be seen if they were present.

It must be recalled that the trilete and monolete (haptotypic) structures of cryptogamic plants are a very definite spore feature, consisting not merely of a ridge which might be abraded from an otherwise featureless surface, but actually consisting of two margins, sometimes thickened, and a definite suture line between them which cannot be removed except by abrasion of the whole thickness of the proximal wall of the spore.

Thiessen also fails to make any mention of the punctations which are so characteristic of the thicker walled forms referable to *Tasmanites*, and which are definitely but rather crudely shown in the illustrations of Johnson and Thomas. Had he appreciated what they were, it is doubtful that he would have been so positive that these fossils were spores of pteridophytes, because certainly no known spores of pteridophytes possess such structures.

The most recent paper bearing on the subject concerns an examination of Tasmanian oil shale by Singh (1932). He considered that he was examining material similar to that studied by Newton in 1875 which contained *Tasmanites punctatus*. However, from the discrepancy in results it may be that he was dealing

with a different microfossil assemblage. Some of Singh's specimens without doubt are bona fide plant spores. However, he found many forms with about the same shape and size proportions as *T. punctatus* but was unable to see any of the punctae. Trilete markings were clearly visible in some but for others he suggests they "seem to have been rubbed off during fossilization." This, of course, seems quite improbable since the trilete suture lines, if present, cannot be removed by fossilization. Of the figures presented by Singh, actually only one (fig. 3) shows convincing evidence of the trilete marking. The proportions of this specimen suggest *Calamospora* and it is interesting to note that *Phyllotheeca* (a calamarian) is associated in the same strata. Those shown in his figures 7 and 8 are inconclusive as to the presence of a trilete structure, since *Tasmanites* may occasionally be folded under compression to simulate a trilete marking; but careful observation will distinguish the absence of a definite suture line. Since Singh has not shown these structures, actually the only great discrepancy between Newton's and Singh's observations with respect to the more common forms concerns the punctae.

American *Tasmanites* forms show considerable variation in the frequency of punctae and this may be a useful means of specific discrimination. One can scarcely doubt their existence in Newton's original material, because Reinsch also figured them from the Tasmanite material provided from the British Museum and also used and figured additional specimens from Newton's own preparations. So far as the discrepancy in presence of a trilete mark on some specimens is concerned, it must be noted that Reinsch (II, 1884, p. 5) also found "Rarissime occurrent *Triletes* minores singuli interspersi" in Newton's original material. Furthermore, the way Newton's description in general tallies with the verified characters seen in American *Tasmanites* is so striking as to leave no doubt as to the essential correctness of his description.

The surprising thing about American assemblages containing *Tasmanites* is that, so far as is known to be true, no trilete forms (excepting *Foerstia*) have yet been found to occur with them in the assem-

blage. That Reinsch and Singh have found a few trilete spores associated with *Tasmanites* is not to be wondered at. The writers are convinced that, despite associations of this sort, *Tasmanites* does not now, and never has had, any trilete marking on its wall. Lack of this feature is conclusive evidence that *Tasmanites* does not represent any group of ordinary pteridophytic plants.

Discussion.—There are many sporangite forms which do not qualify as species of *Tasmanites*, or any other genus yet designated. Aside from Lang's paper there has been no attempt to report on isolated actual bona fide plant microfossils of similar age. Until more reports are available and greater knowledge has been obtained, it does not seem essential to give further taxonomic consideration to the few that are known. The correlation and coordination of taxonomic groups identified by means of spores from the Devonian, with those groups based on spores which we are utilizing for Carboniferous material, deserves very thorough study and consideration. The abundant plant record that can be obtained may, if advisedly interpreted, have much significance in tracing lines of phyletic relationship among plants. The results that may possibly accrue from study of the problematic microfossils, among which is *Tasmanites*, is hard to predict, although such study cannot fail to at least outline their stratigraphic usefulness.

It needs to be stressed, however, that *Tasmanites*, and other unicentric microfossils certainly do not belong to the well known groups of primitive higher plants that were contemporaneous with them. Their morphologic nature is, in fact, so uncertain that their reference to the plant kingdom would not seem assured except for their chemical composition. Zetzsche, et al., (1931) seem to have definitely proved the absence of nitrogen from authentic *Tasmanites* and furthermore shown their composition to be in general similar to unquestioned fossil plant spores. Though possibly chitinous in appearance, lack of nitrogen apparently eliminates the animal kingdom from consideration. Spores of *Parka* which evidently is a thalloid plant, evidently lack any haptotypic structures (Don and Hickling, 1915) but in no other particular do

they correspond to *Tasmanites*. In fact, these microscopic fossil bodies represent about as great a realm for speculation now as they ever did as to their actual nature and affinity, but this can hardly be represented as a valid excuse for their continued neglect. By strict application of systematic principles we shall approach much nearer a useful understanding of them.

The following list includes names which have been used and will have to be considered in subsequent treatment of species of *Tasmanites*; forms identified as *Sporangites jacksoni* White (1905) and *S. radiatus* Duden (1897) have nothing to do with *Tasmanites* and are omitted on this account.

1. TASMANITES CHICAGOENSIS (Reinsch) S. W. and B., comb. nov.⁵

Discieae, Subtribus I, Subdividio 1., 18. (. addita est nomen Specificum "Chicagoense") Reinsch, 1884. Micro-Paleophytologia, vol. 2, p. 6, pl. 72A, fig. 76.

Named from material supplied by Thomas, the specific name must be credited to Reinsch and the type is the specimen he figured. Dawson (1888b) and Jongmans (1930) erroneously cite Thomas as its author.⁶

2. TASMANITES HURONENSIS (Dawson) S. W. and B., comb. nov.

Sporangites huronensis Dawson, 1871, Am. Jour. Sci., 3rd Ser., vol. 1, no. 4, p. 257, figs. 1-3.

The following description is from the most complete account given by Dawson (1886) in which he corrected some of the earlier inaccuracies. It has also been changed slightly in accordance with the present conception of his material. Definite descriptive data is essentially unaltered. This is presented with the hope that it may be useful until Dawson's type material or authentic topotype material can be reexamined.

Flattened disc-like bodies with smooth rounded edges, usually ranging from 250 to 350 microns in diameter, showing slight external evidence of punctuation but by transmitted light at higher magnification exhibiting numerous pores which penetrate the wall. Sometimes marked by characteristic rounded folds or split open by compression. By transmitted light they appear amber colored, or sometimes have a reddish hue; in section the walls show faint indications of concentric lamination. The walls are moderately thick, 1/10 to 1/20 of the total diameter. They never exhibit the triradiate marking seen in spores of lycopods. The interior is usually vacant but in some cases more or less filled with mineral matter (very fine pyritic crystals, calcite, etc.).

⁵ The initials S. W. and B. used here and elsewhere throughout this paper refer to the present authors, Schopf, Wilson, and Bentall.

⁶ A copy of the Micro-Paleophytologia originally owned by Thomas now in the John Crerar Library in Chicago, has the inscription "Chicagoensi of B. W. Thomas," written on two of the figures, one of which is not Reinsch's No. 18. Thomas thus may have interpreted his material a little differently than Reinsch did and may have misunderstood the taxonomic principles involved. The primary purpose of author citation is to indicate type material upon which the description is based.

3. TASMANITES PUNCTATUS Newton, 1875, Geol. Mag., ser. 2, vol. 2, no. 8, p. 341, pl. 10, figs. 2, 8.

The type species of *Tasmanites*. (See description as previously quoted from Newton.)

4. TASMANITES spp. Reinsch, nos. 12, (p. 3); 17, (pp. 3-4); 26, (p. 5); 32, (p. 6) and 65 (?), (p. 9); 1884, Micro-Paleophytologia.

Reinsch's diagnoses and illustrations suggest the numbers listed above, based on American, Australian, and Tasmanian material, are probably referable to *Tasmanites*. Although others he assigned to the Discieae also lack haptotypic spore features, they are probably generically dissimilar.

Note.—There is a possibility that the isolated bodies associated with *Protosalvinia brasiliensis* Dawson and *P. bilobata* Dawson are referable to *Tasmanites*, and if so, they should receive separate taxonomic consideration and not be assigned to *Protosalvinia*. *Protosalvinia clarkei* Dawson, which was originally identified with *Tasmanites huronensis* (Dawson) by Clarke (1885) probably is entirely different and deserves restudy. One would judge that *Tasmanites* also occurs associated with this material. Probably many of the "Sporangites" occurrences given by Williams (1887) and various other authors are referable to *Tasmanites* but a critical reexamination of all of this material is needed.

The forms designated as *Sporangites alaskensis* and *Sporangites arctica* by David White (1929) were studied only from thin sections. The former shows wall peculiarities which may be comparable to that of *Tasmanites*; the latter appears very similar to sectioned spores of higher plants. Whether the breaks in the walls are accidental (as they would be in *Tasmanites*) or are due to the section transecting a definitely organized suture of a spore coat is difficult if not impossible to determine from sections alone. This material was considered possibly Lower Cretaceous in age and a definite identification of *Tasmanites* would be of considerable interest.

Genus TRILETES (Reinsch, 1884); Schopf emend., 1938.

Plate 1, figures 2, 2a, 3, 3a

Megaspores radially symmetrical; proximal side marked by triradiate sutures, often with arcuate ridges connecting the ends of the rays; distal surfaces smooth or variously ornamented. Ornamentation generally less well developed on proximal than on distal surfaces. Spores are relatively very large up to more than 3 mm. Affinity with the free-sporing lycopods. Type species, by designation, *Triletes reinschi* (Ibrahim) Schopf (1938).

This genus is a large and important one in classification of fossil spores, particularly in the Carboniferous period when the free-sporing lycopods were

dominant. Evidence of the affinity of these spores is shown by every spore-containing megasporangiate fructification of the free-sporing lycopsids of this period. Unfortunately, this corollary information has not always been considered in fossil spore classification and additional genera have been proposed which are in conflict with *Triletes*. The types of these subsequently defined and consequently untenable genera are listed below. They are also included in alphabetical position in the main list of species with their synonymous citations.

Triletes reinschi (Ibrahim) Schopf (1938), which also is the type species by designation for *Triletes*. (Type of *Laevigatisporites* Ibrahim 1933).

Triletes tuberosus (Ibrahim) S. W. and B., comb. nov. (Type of *Tuberculatisporites* Ibrahim, 1933).

Triletes sextus S. W. and B., nomen nov. (As *Triletes* VI of Bennie and Kidston (1886), this form was regarded as the type of *Apiculatisporites* Ibrahim, 1933).

Triletes hirsutus (Loose) S. W. and B., comb. nov. (Type of *Setosi-sporites* Ibrahim, 1933).

Triletes sextusdecimus S. W. and B., nomen nov. (As *Triletes* XVI of Bennie and Kidston (1886), this form was regarded as the type of *Zonales-sporites* Ibrahim, 1933).

Triletes trilobus (Ibrahim) S. W. and B., comb. nov. (Type of *Valvisi-sporites* Ibrahim, 1933).

By no means all the species that authors regarded as congeneric with these types by virtue of arbitrary (artificial) distinctions appear so when broader comparisons are attempted. This is particularly true of the smaller forms (isospores and microspores) which often have been denominated indiscriminately. These forms have of course been reallocated to what have the appearance, at least, of constituting more natural groups.

The following is a list of described species of *Triletes* as the genus is now conceived. Some forms listed here may be so closely related to one another that in later studies the names will be considered as synonyms. Without consultation of the types or specimens corresponding to them these questions as to actual synonymy appear to be unsolvable. Wicher (1934) has placed several of these names in synonymous relationship, and in all probability correctly, since many of the poorly illustrated holotypes were available

to him for examination. It may be likewise a matter of individual opinion as to whether certain holotypes are conspecific. Such questions tend to be academic because there can be no doubt that the relationship is close in these instances. Also, whether the forms are distinguished as species or as varieties may be a matter of individual taxonomic policy. We have made as few changes of status as seemed reconcilable with a uniform taxonomic practice. Inconsistencies too may be found here, but it is hoped that these are within permissible limits of individual opinion.

The synonomies are not absolutely complete in the sense that references to all forms that have ever been described or illustrated are included because triletean forms are represented in too many published illustrations for them all to be cited. The chief concern has been to give the references which include the type material or throw light upon it. Other references incidental to this purpose are given in a good many instances, chiefly to indicate the general features of occurrence, both stratigraphic and geographic.

Stratigraphic distribution has been generally given for each. Such ranges are always subject to revision for a number of reasons. Many have been taken from the stratigraphic distribution tables and discussion published by Zerndt (1931, p. 169; 1937a, p. 68; 1937b, p. 590, 593; 1938; 1940, p. 142). The correlation chart given by Gothan (1937, p. 299) has been helpful in understanding the relative position of the mostly unfamiliar named units of the Polish and Lower Silesian stratigraphic succession. Approximate equivalence of European and American Carboniferous divisions are given in the chart previously published by one of us (Schopf, 1941, p. 9). Zerndt's data on stratigraphic distribution is much more extensive than information from any other source and consequently deserves most serious consideration. Doubtless many forms not reported by him have a greater stratigraphic range than has been recognized. Zerndt's data, however, are given for his spore "types" rather than for species. Most of his types and species have general equivalence yet this is not true in all cases and some discrepancy may occur on this account. In general,

probably a good many specific determinations have not been rendered critically enough and this also tends to diminish the value of stratigraphic ranges which can be given now. Nevertheless, some general information may be gained from the ages listed. It has been observed that a good many of the distinctive forms appear in the same relative positions in America and in the European Carboniferous (Schopf, chiefly unpublished data) which gives promise of future assistance in long distance correlation.

Ninety-five species are included here. Many of them are referable to the sections of *Triletes* already proposed (Schopf, 1938); others are less definitely assigned. Certain relationships between species have been noted when these seemed particularly evident. *Triletes* is by no means an exclusively Paleozoic genus and Mesozoic forms have also been included for sake of completeness. Several new names have been proposed here, in addition to the considerable number of new combinations required in order to follow a consistent and relatively uniform taxonomic policy.

1. *TRILETES AGNINA* (Zerndt) S. W. and B., comb. nov.

Lagenicula agnina Zerndt, 1937, Acad. polonaise sci. Trav. Geol. no. 3, p. 14, pls. 21-22.

Type 34 Zerndt, 1937, idem.

Sectio, *Lagenicula*. Age, Lower Namurian (Flora series).

2. *TRILETES ALES* Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, p. 163, fig. 53A-E, pl. 25, figs. 2, 8, 9, 11.

Age, Liasso-Rhaetic.

3. *TRILETES ANGULATA* (Zerndt) S. W. and B., comb. nov.

Lagenicula angulata Zerndt, 1937, Acad. polonaise sci. Trav. Geol. no. 3, pp. 11-12, fig. 8, pls. 14, 15.

Type 7 Zerndt, 1931, Acad. polonaise sci. Bull. internat., ser. A, p. 171, pl. 3, fig. 8.

Sectio, *Lagenicula*. Age, Lower Namurian (Grodziec series).

4. *TRILETES AREOLATUS* Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, pp. 158-159, fig. 51A-F, pl. 26, figs. 3, 10.

Age, Liasso-Rhaetic.

5. *TRILETES ARIADNAE* (Miner) Harris, 1935, idem, p. 155.

Selaginellites ariadnae Miner, 1932, Washington Acad. Sci. Jour., vol. 22, p. 505, figs. 26-30.

Age, Upper Cretaceous.

6. *TRILETES ARNOLDI* (Miner) Harris, 1935, Meddelelser om Grönland, vol. 112, p. 155.

Selaginellites arnoldi Miner, 1932, Washington Acad. Sci. Jour., vol. 22, p. 500, figs. 22-25.

Age, Upper Cretaceous.

7. *TRILETES AUGUSTAE* (Loose) S. W. and B., comb. nov.

Zonales-sporites augustae Loose, 1934, Inst. Paläobot. Arb. vol. 4, p. 150, pl. 7, fig. 32.

Sectio, *Auriculati?* Age, Westphalian B (Gasflamm).

8. *TRILETES AURANTIIUM* Harris, 1935, Meddelelser om Grönland, vol. 112, No. 1, pp. 164-165, fig. 52H-L, pl. 25, fig. 5, pl. 26, fig. 5.

Age, Liasso-Rhaetic.

9. *TRILETES APICULATUS* (Ibrahim) S. W. and B., comb. nov.

Apiculati-sporites apiculatus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 23, pl. 5, fig. 31.

Type 14 Zerndt (in part), 1931, Acad. polonaise sci. Bull. internat., ser. A, p. 172; 1935, Acad. polonaise sci. Trav. Geol. no. 1, pp. 17-18.

Sectio, *Aphanozonati*. Age, Lower Namurian, Westphalian B, and younger (?).

10. *TRILETES ARTECOLLATUS* Nowak and Zerndt, 1936, Acad. polonaise sci. Bull. internat., ser. A, p. 58, pl. 1, figs. 4, 5.

Type 39, Zerndt, 1936, idem.

Sectio, *Triangulati*. Age, Dinantian (Raczna Series).

11. *TRILETES AURITUS* Zerndt, 1930, idem, ser. B, p. 46, pl. 1, figs. 4 and 5.

Spore 0.7 mm. Zerndt, 1930, Soc. geol. Pologne Ann., vol. 6, pp. 307-308, 312, pl. 1, figs. 3a, b, pl. 3, figs. 3a-d.

Types 11 and 12 Zerndt, 1931, Acad. polonaise sci. Bull. internat., ser. A, p. 172.

Triletes auritus Zerndt, 1937, idem, p. 584, pl. 10, figs. 2, 6.

Triletes auritus Zerndt, 1940, Paleontographica, vol. 84, abt. B, p. 146, pl. 9, figs. 5-18.

Sectio, *auriculati* (type). Age, Westphalian C, D.

TRILETES AURITUS var. *GRANDIS* Zerndt, 1937, Acad. polonaise Bull. internat., ser. A, p. 584, pl. 10, figs. 1, 3-5.

Type 11a, Zerndt, 1937 (see above).

Triletes auritus var. *grandis* Zerndt, 1940, Paleontographica, vol. 84, abt. B, p. 134, pl. 11, figs. 32-35.

Age, Stephanian (Westphalian D?).

TRILETES AURITUS var. *SECUNDUS* (Maslankiewiczowa) S. W. and B., nom. nov.

- Triletes auritus* II Maslankiewiczowa, 1932, Acta Soc. Bot. Polonaise, vol. 9, (Suppl.), p. 158-161, figs. 33-36.
12. TRILETES APPENDICULATUS Maslankiewiczowa, 1932, idem., p. 163-164, fig. 39.
Type 12 Zerndt, 1937 (non 1931), Acad. polonaise sci. Trav. Geol. no. 3, p. 3.
Type 6 Sahabi, 1936, Recherches sur les spores des houilles Francaises, p. 39-40, pl. 2, fig. 5.
Type 8? Sahabi, 1936, Recherches sur les spores des houilles Francaises, p. 41, pl. 2, figs. 7-8.
Sectio, *Auriculati*. Age, Westphalian C, D, Stephanian.
13. TRILETES BENNHOLDI Zerndt (non Bode), 1937, Acad. polonaise sci. Trav. Geol. no. 3, p. 5-6, fig. 3, pl. 2, figs. 1-6.
Type 33 Zerndt, 1937 (idem).
Porosporites bennholdi (Bode) Zerndt, 1938, Deuxieme Cong. Stratig. Carbonif., vol. III. p. 1713. Age, Lower Namurian (Flora series).
- Note.—Zerndt credited this specific epithet to Bode, apparently assuming the spores conspecific with those of *Porostrobus bennholdi*. If *Porostrobus* can be identified reliably from its isolated spores alone, then evidently *Porostrobus* is a later homonym of *Triletes*. Such is hardly the case, however, because the identification of the genus *Porostrobus* and the species *bennholdi* within it depend on other features in addition to the spores. Some day we possibly may know actually how diagnostic isolated spores of *Porostrobus* may be, but at present such specimens certainly must be recorded separately under a different genus (as Zerndt has done). Consequently, also, these forms must be identified with reference to different nomenclatural types. The specimen illustrated by Zerndt's photograph 4, plate 2, and which evidently served as the basis for his text figure 3 (p. 6), is regarded as the holotype of the species which is here credited to Zerndt.
- On the other hand, no question arises as to the spores Wicher (1934b) described in some detail that were isolated from undisputed specimens of *Porostrobus*. There was no occasion for him to assign them a new generic name (*Poro(strobo)sporites*) since the only possible designation for the specimens is "spores of *Porostrobus bennholdi*." Zerndt, in using the name "*Porosporites*" in 1938, is presumably following Wicher. Wherever evidence of additional cone characters warrants it, such a determination is more significant and essentially useful than identification with a less closely defined group such as *Triletes*. Mistakes of this kind are less likely to occur if nomenclatural types are regarded seriously.
14. TRILETES BIPILOSUS (Wicher) S. W. and B. comb. nov.
Sporites bipilosus Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 180, pl. 8, figs. 13, 14.
- Sectio, *Lagenicula*. Age, Lower Westphalian C.
- Note.—This species is apparently closely related to *Triletes robertianus* and *T. latihirsutus*.
15. TRILETES BOREALIS (Miner) Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, p. 155.
Selaginellites borealis Miner, 1932, Washington Acad. Sci. Jour., vol. 22, p. 503, figs. 12-21.
16. TRILETES BRASSERTI Stach and Zerndt, 1931, Glückauf, Jahrg. 67, no. 35, p. 1123, figs. 29, 30, (?) 31.
Type 20 (*Triletes brasserti* Stach and Zerndt), Zerndt, 1934, Acad. polonaise sci. Trav. Geol., No. 1, pp. 23-24, fig. 9, pl. 25, figs. 1-2. Age, Dinantian, Namurian Westphalian A, B.
Note.—Closely related to *Triletes circumtextus*, *T. saturnoides* and *T. superbus*.
17. TRILETES BREVIACULEATUS Nowak and Zerndt, 1937, Zerndt, idem., no. 3, pl. 4, figs. 1, 2.
Type 38, *Triletes breviaculeatus* Nowak and Zerndt, 1936, Acad. polonaise Bull. internat., ser. A, p. 57.
Sectio, *Aphanozonati*. Age, Upper Dinantian (Raczna series), Lower Namurian (Flora series).
Note.—Evidently by mistake an illustration of *Triletes horridus* accompanied Nowak and Zerndt's original description. The species was validated by photographs published a year later.
18. TRILETES BREVISPLICULUS Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, pp. 26-27, pl. 1, figs. 13a-r; pl. 2, fig. 6; pl. 3, figs. 1-4.
Sectio, *Aphanozonati*. Age, Middle Pennsylvanian, Carbondale series.
19. TRILETES CIRCUMTEXTUS Zerndt, 1934, Acad. polonaise sci. Trav. Geol. no. 1, pp. 19-21, fig. 7; pl. 19, figs. 1-12; pl. 21, figs. 1-7.
Type 18 Zerndt, 1931, Acad. polonaise Bull. internat., ser. A, p. 173, pl. 6, figs. 17, 18.
Age, Lower Namurian.
Note.—Closely related to *Triletes brasserti*.
20. TRILETES CLAVATOPILOSUS (Wicher) S. W. and B., comb. nov.
Sporites clavatopilosus Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 183, pl. 8, figs. 25-26.
Type 24 Zerndt, 1931, Acad. polonaise sci. Bull. internat., ser. B, pp. 174-175, pl. 7, fig. 23.
Type 14 Sahabi (?), 1936, Recherches sur les spores des houilles Francaises, pp. 47 and 48, pl. 6, figs. 5-7. Age, Upper Westphalian A—Lower Westphalian C.
21. TRILETES CRASSIACULEATUS (Zerndt) S. W. and B., comb. nov.
Lagenicula crassiaculeata Zerndt, 1937,

- Acad. polonaise sci. Trav. Geol. no. 3, pp. 12-13.
 Type 26A, Zerndt, 1937 (idem).
 Sectio, *Lagenicula*. Age, Upper Dinantian (?).
Note.—Related to *Triletes horridus*.
22. TRILETES CYTTARIA Kendall, 1942, Annals and Mag. Nat. History ser. 11, vol. 9, p. 922, fig. 2.
 Age, Jurassic (Mid. Estuarine).
23. TRILETES DIFICILIS (Wicher) S. W. and B., comb. nov.
Sporites dificilis Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 179, pl. 8, figs. 17-18.
 Type 14 (in part) Zerndt, 1931 Acad. polonaise sci. Bull. internat., ser. A, p. 172, pl. 4, figs. 11, 12, pl. 5, figs. 15, 16.
 Zerndt, 1934, Acad. polonaise sci. Trav. Geol. no. 1, pp. 17-18, pl. 8, figs. 1-10, pl. 31, figs. 8, 9.
 Sectio, *Aphanozonati*. Age, Lower Westphalian C. (Zerndt, Mid. Lower Namurian to Westphalian D).
24. TRILETES DIFUSOPILOSUM (Wicher) S. W. and B., comb. nov.
Sporites difusopilosus Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, pp. 182-183, pl. 8, figs. 23, 24. Age, Lower Westphalian C.
Note.—Closely related to *Triletes praetextus*.
25. TRILETES ECHINATUS (Miner) Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, p. 155.
Selaginellites echinatus Miner, 1932, Washington Acad. Sci. Jour., vol. 22, p. 500, fig. 6. Age, Upper Cretaceous.
26. TRILETES ERLANSONI (Miner) Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, p. 155.
Selaginellites erlansoni Miner, 1932, Washington Acad. Sci. Jour., vol. 22, p. 500, figs. 1-3. Age, Upper Cretaceous.
27. TRILETES FLAVUS Stach and Zerndt, 1931, Glückauf, Jahrg. 67, no. 35, p. 1122, fig. 18.
 Sectio, *Auriculati*. Age, Westphalian C.
28. TRILETES FULGENS Zerndt, 1937, Acad. polonaise sci. Trav. Geol. no. 3, p. 5, fig. 2, pl. 1, figs. 1-9.
 Type 8 Zerndt, 1931, Acad. polonaise sci. Bull. internat., ser. A, p. 171, pl. 3, figs. 9-10.
 Sectio, *Aphanozonati*. Age, Middle Dinantian to Middle Namurian.
Note.—Closely related to *Triletes glabratus* (pars.).
29. TRILETES GLABRATUS Zerndt, 1930, idem, ser. B, p. 45, pl. 1, figs. 2, 3.
 Type 9 Zerndt, 1931, idem, ser. A, p. 171.
- Sectio, *Aphanozonati*. Age, Westphalian B, C, Lower Stephanian.
Note.—Closely related to *Triletes fulgens* and *Triletes reinschi*.
30. TRILETES GREENLANDICUS (Miner) Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, p. 155.
Selaginellites greenlandicus Miner, 1932, Washington Acad. Sci. Jour., vol. 22, p. 500, figs. 10, 11. Age, Lower Cretaceous.
31. TRILETES GYMNOCERATIS Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, pp. 37-38, pl. 1, fig. 4, pl. 4, fig. 9.
 Sectio, *Triangulati*. Age, Middle Pennsylvanian, Carbondale series.
Note.—Closely related to *Triletes artecolatus*.
32. TRILETES HARRISII Murray, 1939, Geol. Mag., vol. 76, p. 480, figs. 1, 2.
33. TRILETES HIRSUTUS (Loose) S. W. and B., comb. nov.
Sporonites hirsutus, Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 452, pl. 20, fig. 58.
Setosi-sporites hirsutus (Loose) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 26.
Apiculati-sporites hirsutus (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 153.
Sporites hirsutus (Loose) Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 181.
 Sectio, *Lagenicula*? Age, Westphalian B, Lower Westphalian C.
34. TRILETES HORRIDUS (Zerndt) S. W. and B., comb. nov.
Lagenicula horrida Zerndt, 1934, Acad. polonaise sci. Trav. Geol. no. 1, p. 25, fig. 11, pl. 28, figs. 1-5.
 Type 26 Zerndt, 1931, Acad. polonaise sci. Bull. internat., ser. A, p. 175, pl. 9, fig. 28.
 Sectio, *Lagenicula*. Age, Dinantian.
Note.—Closely related to *Triletes crassiaculeatus*.
35. TRILETES INORNATUS (Miner) Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, p. 155.
Selaginellites inornatus Miner, 1932, Washington Acad. Sci. Jour., vol. 22, p. 505, figs. 7, 8. Age, Upper Cretaceous.
36. TRILETES IONTHUS Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, pp. 166-167, 169, figs. 52E, F, G, pl. 26, fig. 8.
37. TRILETES KIDSTONI (Loose) S. W. and B., comb. nov.
Sporonites kidstoni Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 452, pl. 20, fig. 60.

- Laevigati-sporites kidstoni* (Loose) Ibrahim, 1933, Sporenformen des Aegir-horizonts, p. 19.
- Reticulati-sporites kidstoni* (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, pp. 156-7.
- Sectio, *Aphanozonati*. Age, Upper Westphalian B, Lower Westphalian C.
38. TRILETES LATIHIRSUTUS (Loose) S. W. and B., comb. nov.
Apiculati-sporites latihirsutus Loose, 1934, idem, p. 153.
 Sectio, *Lagenicula*. Age, Upper Westphalian B.
 Note.—Closely related to *Triletes robertianus*.
39. TRILETES LAXIMARGINALIS Zerndt, 1940, Paleontographica, vol. 84, Abt. B, p. 136, pl. 10, figs. 24-28.
 Type 17a, Zerndt, 1940 (idem).
 Sectio, *Triangulati*. Age, Westphalian C, D (?).
 40. TRILETES LEVIS (Zerndt) S. W. and B., comb. nov.
Lagenicula levis Zerndt, 1937, Acad. polonaise sci. Bull. internat., ser. A, pp. 587-588, pl. 15, figs. 1-11.
 Type 45 Zerndt, 1937 (idem).
 Sectio, *Lagenicula*. Age, Stephanian.
 Note.—Closely related to *Triletes translucens*, *T. tenuimembranosa* and to *T. rugosus*.
41. TRILETES LITCHI Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, pp. 159, 160, fig. A-F, pl. 26, figs. 3, 10.
 Age, Liasso-Rhaetic.
42. TRILETES MAMILLARIUS Bartlett, 1928, Michigan Acad. Sci., vol. 9, p. 21, pls. 13-15.
 Sectio, *Aphanozonati*. Age, possibly Upper Pottsville or Lower Allegheny.
43. TRILETES MENSURA Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, pp. 160-162, fig. 53J, pl. 26, figs. 2, 9.
 Age, Liasso-Rhaetic.
44. TRILETES MIRABILIS (Miner) S. W. and B., comb. nov.
Selaginellites mirabilis Miner, 1935, Am. Midland Naturalist, vol. 16, p. 618, pl. 23, figs. 1-6. Age, Upper Cretaceous?.
45. TRILETES MUCRONATUS Nowak and Zerndt, 1936, Acad. polonaise sci. Bull. internat., ser. A, p. 59, pl. 1, figs. 1, 2.
 Type 40 Zerndt, 1936 (idem). Age, Dinantian.
 Note.—Possibly closely related to *Triletes clavatopilosus*.
46. TRILETES MYRMECOIDES Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, fig. 52M-Q, pl. 26, fig. 4.
 Age, Liasso-Rhaetic.
47. TRILETES NIGROZONALIS Stach and Zerndt, 1931, Glückauf, Jahrg. 67, no. 35, p. 1123, figs. 26, 27.
Sporites nigrozonalis (Stach and Zerndt) Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, pp. 176-177, pl. 8, figs. 11 and 12.
 Sectio, *Auriculati*. Age, Westphalian C.
48. TRILETES NODOSUS (Wicher) S. W. and B., comb. nov.
Sporites nodosus Wicher, 1934, idem, p. 177, pl. 8, fig. 21.
 Sectio, *Aphanozonati*. Age, Lower Westphalian C.
49. TRILETES NUDUS (Nowak and Zerndt) Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, p. 30, pl. 5, fig. 7.
Lagenicula nuda Nowak and Zerndt, 1936, Acad. polonaise sci. Bull. internat., ser. A, p. 60, pl. 1, fig. 6.
 Type 43 Zerndt, 1936 (idem).
 Sectio, *Lagenicula*. Age, Dinantian.
 Note.—The form recorded from Illinois as *T. (?) nudus* probably is not referable to this species although the shape is rather similar.
50. TRILETES OVALIS Stach and Zerndt, 1931, Glückauf Jahrg. 67, no. 35, p. 1122, fig. 24.
 Age, Westphalian B, Lower Westphalian C.
 Note.—Probably closely related to type 5 of Sahabi (1936)..
51. TRILETES PAPILLOSUS (Miner) Harris, 1935, Meddelelser om Grönland, vol. 112, No. 1, p. 155.
Selaginellites papillosum Miner, 1932, Washington Acad. Sci. Jour., vol. 22, p. 500, fig. 9. Age, Upper Cretaceous.
52. TRILETES PARVIAPICULATUS Zerndt, 1937, Acad. polonaise sci. Trav. Geol. no. 2, p. 17, pl. 24, figs. 1-4.
 Sectio, *Triangulati?*. Age, Lower Marginal beds (Lower Namurian, vicinity of Rybník).
53. TRILETES PEDINACRON Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, pp. 165-166, fig. 52S, T, pl. 27, fig. 6.
 Age, Liasso-Rhaetic.
54. TRILETES PERSIMILIS Harris, 1935, idem., p. 165, fig. 52R, pl. 25, fig. 4.
55. TRILETES PERTUBEROSUS (Loose) S. W. and B., comb. nov.
Sporonites pertuberosus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 452, pl. 20, fig. 57.
Tuberculati-sporites pertuberosus. (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 147, pl. 20, fig. 57.
 Sectio, *Aphanozonati*. Age, Upper Westphalian B.

- Note.*—Equal to Type 14 Zerndt (1931, 1934) in part.
56. *TRILETES PHYLLICUS* Murray, 1939, Geol. Mag., vol. 76, p. 482, figs. 7, 8.
Age, Jurassic (Estuarine).
57. *TRILETES PINGUIS* Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, p. 166, fig. 52A-D, pl. 25, fig. 3.
Age, Liasso-Rhaetic.
58. *TRILETES POLYSCLEES* Murray, 1939, Geol. Mag., vol. 76, p. 484, figs. 5, 6.
Age, Jurassic (Estuarine).
59. *TRILETES PRAETEXTUS* Zerndt, 1934, Acad. polonaise sci. Trav. Geol. no. 1, p. 24, pl. 26, figs. 1-6, pl. 27, figs. 1-6, Text-fig. 10.
Type 21 Zerndt, 1931, Acad. polonaise sci. Bull. internat., ser. A, p. 174, pl. 8, figs. 24, 25.
Age, Upper Dinantian and Lower Namurian.
Note.—Closely related to *Triletes difusopilosus*.
60. *TRILETES POTOSIENSIS* Zerndt, 1938, Deuxième Cong. Stratig. Carbonifère, vol. 3, p. 1728, pl. 155, fig. 4.
Sectio, *Auriculati?*. Age, Carboniferous.
61. *TRILETES RADIATUS* (Ibrahim) S. W. and B., comb. nov.
Sporonites radiatus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 449, pl. 16, fig. 25.
Zonales-sporites radiatus (Ibrahim) Ibrahim, 1933, Sporenformen des Aegir-horizonts, p. 29, pl. 3, fig. 25.
Sectio, *Triangulati*. Age, Aegir coal, at boundary of Westphalian B and C.
62. *TRILETES RADIOSUS* S. W. and B., nom. nov.
Triletes radiatus Zerndt, 1937, Acad. polonaise sci. Trav. Geol. no. 3, p. 10, fig. 7, pl. 13, figs. 1-5.
Types 22 and 23 Zerndt, 1931, Acad. polonaise sci. Bull. internat., ser. A, p. 174, pl. 8, figs. 24, 25.
Age, Lower Namurian (Upper Dinantian?).
Note.—*T. radiatus* Zerndt, 1937, becomes a later homonym in conflict with *Sporonites radiatus* Ibrahim when the latter is transferred to *Triletes* (see sp. 61 above), thus necessitating a new name as here proposed.
63. *TRILETES REINSCHI* (Ibrahim) Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, p. 24, pl. 2, figs. 2-4, pl. 5, figs. 8, 9.
Triletes I Bennie and Kidston, 1886, Royal Phys. Soc. Edinburgh Proc., vol. 9, p. 107, pl. III, figs. 1a, b.
Spore 1.9 mm. Zerndt, 1930, Soc. Geol. Pologne, Ann. vol 6, p. 308, 312, pl. 1, figs. 5a, b, pl. III, figs. 5a, b.
Triletes Type 1 Kidston, Zerndt, 1930, Acad. polonaise sci. Bull. internat., ser. B, p. 43, pl. 1, fig. 1.
- Type 10 Zerndt, 1931, idem., ser. A, p. 172.
Triletes I Kidston, Stach and Zerndt, 1931, Glückauf, Jahrg. 67, no. 35, p. 1122.
Triletes Type 1 Kidston, Maslankiewiczowa, 1932, Acta soc. Bot. polonae, vol. 9 (Suppl.), p. 158.
Sporonites reinschi Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 449, pl. 17, fig. 28.
Laevigatisporites reinschi (Ibrahim) Ibrahim, 1933, Sporenformen des Aegir-horizonts, p. 18, pl. 4, fig. 28.
Reticulatisporites reinschi (Ibrahim) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 157.
Sporites primus Wicher, 1934, idem. no. 4, p. 169.
Types 1 to 6 incl., Rousseau, 1935, Mus. royale histoire nat. Belgique Bull. vol. 11, no. 21, pp. 3-4, pl. 1, figs. 1-5, pl. 2, fig. 6.
Type 1 Sahabi (pars.), 1936, spores des houilles Francaises, p. 34, pl. 1, figs. 1, 2.
Sectio, *Aphanozonati*. Age, Westphalian C & D, Lower Stephanian.
Note.—Type species of *Triletes* by designation (Schopf, 1938).
64. *TRILETES RETICULATUS* Zerndt, 1938, Deuxième Cong. Stratig. Carbonif., vol. 3, p. 1728, pl. 155, fig. 5.
Age, Mesozoic.
65. *TRILETES REXARGENTEUS* Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, pp. 156-158, fig. 51G-J, pl. 26, fig. 13.
Age, Liasso-Rhaetic.
66. *TRILETES RICHARDSONI* Murray, 1939, Geol. Mag., vol. 76, pp. 482-484, figs. 9, 10.
Age, Jurassic (Estuarine).
67. *TRILETES ROBERTIANUS* S. W. and B., nom. nov.
Triletes kidstoni Zerndt, 1934, Acad. polonaise sci. Trav. Geol. no. 1, pp. 26-27, fig. 12, pl. 28, figs. 6-11, pl. 29, figs. 1-13.
Type 27 Zerndt, 1931, Acad. polonaise sci. Bull. internat., ser. A, p. 175, pl. 9, figs. 29-32.
Sectio, *Lagenicula*. Age, Dimantian, Namurian, Westphalian A.
Note.—Closely related to *Triletes bipilosus* and to *T. latihirsutus*. The new name is necessitated by preoccupation of the specific epithet (species no. 37). This species is likewise named for Robert Kidston.
68. *TRILETES ROTATUS* Bartlett, 1928, Michigan Acad. sci. Papers, vol. 9, p. 21, pls. 9, 10, 11, 12.
Type 19, *Triletes rotatus* Bartlett, Zerndt, 1934, Acad. polonaise sci. Trav. Geol. no. 1, pp. 21-22, fig. 8, pl. 24, figs. 1-6.
Triletes rotatus Bartlett, Zerndt, 1937, idem., no. 3, pp. 8-10, pls. 6-10.
Age, type material probably upper Pottsville.

- TRILETES ROTATUS var. DENTICULATA Zerndt, 1937, Acad. polonaise sci. Trav. Geol. no. 3, pp. 9-10, fig. 6 (?), pl. 6, fig. 3.
Age, Dinantian, Lower Namurian and above (?).
69. TRILETES RUGOSUS (Loose) Schopf, 1938, Illinois Geol. Surv. Rept. Inv. 50, pp. 29-30, pl. 5, fig. 6.
Sporonites rugosus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 452, pl. 20, fig. 59.
Lexigati-sporites rugosus (Loose) Ibrahim, 1933, Sporenformen des Aegirhorizonts, pp. 18-19, pl. 7, fig. 65.
Punctati-sporites rugosus (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 146.
Sectio, *Lagenicula*. Age, Upper Westphalian B and above (?).
Note.—May be closely allied with *Triletes translucens*.
70. TRILETES SAARENSIS Zerndt, 1941, Paleontographica, Abt. B, vol. 84, p. 134, pl. 12, figs. 40-44.
Type 47 Zerndt, 1941 (see above reference).
Sectio, *Auriculati* (?). Age, Westphalian C and Lower Westphalian D.
71. TRILETES SATURNOIDES (Ibrahim) S. W. and B., comb. nov.
Sporonites saturnoides Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 449, pl. 16, fig. 26.
Zonales-sporites saturnoides (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 27-28, pl. 3, fig. 26.
Age, Upper Westphalian B.
Note.—Allied with *Triletes brasserti*, *T. superbus* and *T. circumtextus*.
72. TRILETES SEXTUS S. W. and B., nom. nov.
Triletes VI Bennie and Kidston, 1886, Royal Physical Soc. Edinburgh Proc., vol. 9, p. 109, pl. 3, figs. 6a, 6b, 6c.
Sectio, *Aphanozonati*. Age, Lanarkian=Namurian.
Note.—Forms of this sort are included by Zerndt (1931, 1934) in Type 14. Inasmuch as this was used as the type for *Apiculati-sporites* Ibrahim, it seems desirable to have an orthodox designation for reference.
73. TRILETES SEXTUSDECIMUS S. W. and B. nom. nov.
Triletes XVI Bennie and Kidston, 1886, idem, pp. 113-114, pl. 5, figs. 16a, 16b, 16c, 16d, 16e.
Age, Bernician and Lanarkian = approx. Upper Dinantian and Namurian.
Note.—Related to *Triletes superbus*, and prob. to *T. circumtextus* and *T. brasserti*. This form was taken as the type of *Zonales-sporites* Ibrahim, hence it seems desirable to propose an orthodox name for purposes of reference.
74. TRILETES SILVANUS (Ibrahim) S. W. and B., comb. nov.
Sporonites silvanus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 448, pl. 15, fig. 22.
Laevigati-sporites silvanus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 20, pl. 2, fig. 22, pl. 6, fig. 47.
Sporites silvanus (Ibrahim) Wicher, 1934, Inst. Paläobot. Arb., vol. 4, No. 4, p. 174, pl. 8, figs. 5-8.
Sectio, *Auriculati*. Age, Upper Westphalian B, Lower Westphalian C.
Note.—Closely related to *Triletes auritus*.
75. TRILETES SIMPLEX (Zerndt) S. W. and B., comb. nov.
Lagenicula simplex Zerndt, 1937, Acad. polonaise sci. Trav. Geol. no. 3, pp. 14-15, fig. 10, pl. 23, figs. 1-5.
Type 35 Zerndt, 1937, idem.
Sectio, *Aphanozonati* (?). Age, Lower Namurian.
TRILETES SIMPLEX var. LEVIS Zerndt, 1937, idem., p. 15.
Type 36 Zerndt, 1937, idem.
76. TRILETES SOFIAENSE S. W. and B., nom. nov.
Triletes auritus III Maslankiewiczowa, 1932, Acta Soc. Botanicarum Poloniae, vol. 9 (Suppl.) pp. 161-163, 172-173, figs. 37, 38.
Sectio, *Auriculati*. Age, Upper Westphalian B (Laziska series).
Note.—The group is clearly distinguished specifically by coarse reticulation, in this respect somewhat similar to *Triletes tuberculatus*, though in shape it resembles *Triletes auritus*. Possibly it represents a connecting link between these species. It is named for Zofja Kowalewska Maslankiewiczowa who provided an ample description of the form.
77. TRILETES SPARASSUS Murray, 1939, Geol. Mag., vol. 76, p. 480, p. 482, figs. 3, 4.
Age, Jurassic (Estuarine).
78. TRILETES SPLENDIDA (Zerndt) S. W. and B., comb. nov.
Lagenicula splendida Zerndt, 1937, Acad. polonaise sci. Trav. Geol. no 3, pp. 13-14, pls. 18-20.
Type 28 Zerndt, 1931, Acad. polonaise sci. Bull. internat., Ser. A, p. 175, pl. 10, figs. 36, 37.
Sectio, *Aphanozonati*. Age, Upper Dinantian, Lower Namurian.
Note.—The lageniculate vestibule possessed by this form is insufficient basis for assigning it to *Lagenicula* in disregard of its other characteristic *Aphanozonati* features.
79. TRILETES STENOXYSMATODES Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, p. 167, pl. 25, fig. 6.
Age, Liasso-Rhaetic.
80. TRILETES SUBFUSCUS (Wicher) S. W. and B., comb. nov.

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- Sporites subfuscus* Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 179, pl. 8, fig. 20.
 Type 14 Zerndt (in part), 1934, Acad. polonaise sci. Trav. Geol. no. 1, pp. 17, 18, fig. 5, pls. 8-17.
- Sectio, *Aphanozonati*. Age, Lower Westphalian C.
81. TRILETES SUBROTUNDUS (Miner) Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, p. 155, p. 165.
Selaginellites subrotundus Miner, 1932, Washington Acad. Sci. Jour., vol. 22, p. 505, figs. 4, 5.
 Age, Upper Cretaceous.
82. TRILETES SUBTILINODULATA (Nowak and Zerndt) S. W. and B., comb. nov.
Lagenicula subtilinodulata, Nowak and Zerndt, 1936, Acad. polonaise sci. Bull. internat., ser. A, pp. 59-60, pl. 1, fig. 7.
 Type 42 Zerndt, Nowak and Zerndt, 1936 (idem).
 Sectio, *Lagenicula*. Age, Dinantian.
83. TRILETES SUBPILOSUS (Ibrahim) S. W. and B., comb. nov.
Setosi-sporites subpilosus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 27, pl. 5, fig. 40.
 Sectio, *Lagenicula*. Age, Aegir coal, boundary of Westphalian B and C.
 Note.—May be closely related to *Triletes robertianus*.
84. TRILETES SUPERBUS Bartlett, 1928, Michigan Acad. Sci. Papers, vol. 9, pp. 20, 21, pl. 7, figs. 1, 2, pl. 8, figs. 1, 2.
 Age, Probably upper Pottsville.
 Note.—Probably allied with *Triletes circumtextus* and *T. brasserti*.
85. TRILETES TENUICOLLATUS Nowak and Zerndt, 1936, Acad. polonaise sci. Bull. internat., ser. A, p. 59, pl. 1, fig. 3.
 Type 41 Zerndt, Nowak and Zerndt, 1936 (idem).
 Age, Dinantian.
86. TRILETES TENUIMEMBRANOSA (Zerndt) S. W. and B., comb. nov.
Lagenicula tenuimembranosa Zerndt, 1937, idem. p. 587, pl. 14, figs. 1, 2.
 Sectio, *Lagenicula*. Age, Westphalian C and Lower Westphalian D.
 Type 25 Zerndt, 1931, idem., p. 175, pl. 9, figs. 33 and 35.
 Sectio, *Lagenicula*. Age, Lower Namurian and Westphalian A.
 Note.—Closely related to *Triletes translucens*.
87. TRILETES TENUISPINOSUS Zerndt, 1934, Acad. polonaise sci. Trav. Geol. no. 1, p. 16, text-fig. 4, pl. 7, figs. 1-15.
 Type 13 Zerndt, 1934 (idem).
- TRILETES TENUISPINOSUS var. BREVISPINOSA Zerndt, 1937, idem., no. 3, p. 6, fig. 4, pl. 3, figs. 2-7.

TRILETES TENUISPINOSUS var. SECUNDUS S. W. and B., var. nom. nov.

Triletes tenuispinosus var. II Zerndt, 1937, idem., no. 3, pp. 7-8, fig. 5, pl. 3, figs. 3 and 4. Age, Dinantian — Upper and Lower Namurian.

Note.—Zerndt describes three forms, one which evidently is typically the species and two varieties, only one of which is properly named. The new varietal name proposed provides a means of reference.

88. TRILETES TRANSLUCENS Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, pp. 28-29, pl. 5, figs. 3-5.

Sectio, *Lagenicula*. Age, Middle Pennsylvanian, upper Carbondale, lower McLeansboro series.

Note.—Closely related to *Triletes tenuimembranosa*, *T. levius*, and (?) *T. rugosus*.

89. TRILETES TRIANGULATUS Zerndt, 1930, Acad. polonaise sci. Bull. internat., ser. B, p. 51, pl. 7, figs. 19-24.

Spore 0.5 mm. Zerndt, 1930, Soc. Geol. Pologne Ann., vol. 6, pp. 306, 312, pl. 1, figs. 1a, b, c, pl. 2, figs. 1a, b.

Type 17 Zerndt, 1931 Acad. polonaise sci. Bull. internat. ser. A, p. 173.

Sporonites regalis Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 449, pl. 16, fig. 24.

Sporites triangulatus "var. *regalis*" (Zerndt) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 29, pl. 3, fig. 24.

Sporites regalis (Ibrahim) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 149, pl. 7, fig. 34.

Sporites triangulatus (Zerndt) Wicher, 1934, idem, vol. 4, no. 4, p. 175.

Triletes triangulatus Zerndt, 1934, Acad. polonaise sci. Trav. Geol. no. 1, p. 19, fig. 6, pl. 18, figs. 1-24.

Triletes triangulatus Zerndt, Schopf, 1936, Illinois Acad. Sci., Trans. vol. 28, p. 107, fig. 6.

Type X Sahabi, 1936, spores des houilles Françaises, p. 43, fig. 11, pl. 4, figs. 6-11.

Triletes triangulatus Zerndt, 1937, Acad. polonaise sci. Trav. Geol. no. 3, pl. 5, figs. 1-5.

Triletes triangulatus Zerndt, Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, pp. 32-37, pl. 1, figs. 7, 8, pl. 4, figs. 1-7, pl. 7, figs. 5, 6.

Triletes triangulatus Zerndt, 1940, Paleontographica, vol. 84, Abt. B, pl. 10, figs. 19-23.

TRILETES TRIANGULATUS var. ZONATUS (Ibrahim) Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, p. 34.

Triletes triangulatus II Zerndt, 1930, Acad. polonaise sci. Bull. internat., ser. B, p. 53, pl. 7, figs. 25-30.

Sporonites zonatus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 448, pl. 16, fig. 23.

Zonales-sporites triangulatus secundus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 30, pl. 3, fig. 23, pl. 7, fig. 64.

- Zonales-sporites zonatus* (Ibrahim) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 150, pl. 7, fig. 31.
- Sporites triangulatus* var. *zonatus* (Ibrahim) Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, pp. 175-176.
- TRILETES TRIANGULATUS var.?
- Triletes triangulatus* III, Stach and Zerndt, 1931, Glückauf, Jahrg. 67, no 35, p. 1123, figs. 32, 33.
- Sectio, Triangulati.* Age, upper Lower Namurian through Westphalian D.
90. TRILETES TRICOLLINUS Zerndt, 1938, Deuxième Cong. Stratig. Carbonif. vol. 3, p. 1713, pl. 155, fig. 3.
- Type 44 Zerndt, 1938 (idem).
- Sectio, Triangulati.* Age, Westphalian B, C, and D.
91. TRILETES TRILOBUS (Ibrahim) S. W. and B., comb. nov.
- Sporonites trilobus* Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 449, pl. 17, fig. 30.
- Valvisi-sporites trilobus* (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 33, pl. 4, fig. 30.
- Valvisi-sporites trilobus* (Ibrahim) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 152, pl. 17, fig. 30.
- Sectio, Auriculati.* Age, Upper Westphalian B.
- Note.*—Possibly very closely related to *Triletes appendiculatus*. Wicher (1934) regards it as similar to *T. auritus*.
92. TRILETES TUBERCULATUS Zerndt, 1930, Acad. polonaise sci. Bull. internat. ser. B, pp. 47-51, pl. 2, figs. 6, 7, pl. 3, figs. 8, 9, pl. 4, figs. 10, 11, pl. 5, figs. 12, 13.
- Triletes XIX* Kidston, 1890, Royal Soc. Edinburgh Trans., vol. 36, pl. figs. 9-11.
- Type 16 Zerndt, 1931, Acad. polonaise sci. Bull. internat., ser. A, p. 173.
- Triletes tuberculatus* Zerndt, Maslankiewiczowa, 1931, Acta Soc. Bot. Poloniae, vol. 9, Suppl. pp. 165-168, figs. 40, 41.
- Sectio, Auriculati.* Age, Westphalian B, C, Stephanian?
93. TRILETES TUBEROSUS (Ibrahim) S. W. and B., comb. nov.
- Sporonites tuberosus* Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 449, pl. 16, fig. 27.
- Tuberculati-sporites tuberosus* (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 23, pl. 3, fig. 27.
- Tuberculati-sporites tuberosus* (Ibrahim) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 147, pl. 7, fig. 37.
- Sporites tuberosus* (Ibrahim) Wicher, 1934, idem, vol. 4, no. 4, pp. 177-178, pl. 8, fig. 22.
- Sectio, Aphanozonati.* Age, Upper Westphalian B, Lower Westphalian C.
- Note.*—Probably the same as some of Zerndt's Type 14.
94. TRILETES TYLOTUS Harris, 1935, Meddelelser om Grönland, vol. 112, no. 1, pp. 162-163, fig. 53F-I, pl. 26, figs. 1, 12.
Age, Liasso-Rhaetic.
95. TRILETES VALENS (Wicher) S. W. and B., comb. nov.
- Sporites valens* Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 178, pl. 8, fig. 19.
- Sectio, Aphanozonati.* Age, Lower Westphalian C.
- TRILETES nomen excludende
1. *Apiculati-sporites megastiposus* Ibrahim, 1933, Sporenformen des Aegirhorizonts, etc., p. 24, pl. 8, fig. 69.
Note: This form is not congeneric with the type of *Apiculati-sporites* (*Triletes sextus*) and, although it apparently is sufficiently characterized and characteristic to be a useful microfossil, no further generic assignment will be attempted.

Genus PITYOSPORITES Seward, 1914

Plate 2, figures 15-15b

Diagnoses given by Seward are as follows:

The generic designation *Pityosporites* is proposed for winged spores agreeing in form and size with recent Abietineous genera (1914, p. 23).

. . . Spores provided with bladder-like extensions of the exine, agreeing in size and form with those of recent Abietineous genera (1919, p. 398).

A more adequate definition inferred from the above, and from consideration of the species included here, is as follows:

Symmetry.—Pollen grains appearing bilateral, due to the presence of bladders placed on opposite sides. The fundamental symmetry, shown by the body but modified, is radial, as this pollen arises from tetrahedral tetrads.

Shape.—Grains elliptical as viewed from proximal side, the diameter of the poles of the ellipse (formed by the two bladders) being broader than that of the body between them. Body appears approximately circular in proximal view. Viewed from either side the bulbous bladders are inclined distally and a broad sulcus appears between them on the distal side. In lateral outline the body appears broadly oval with the smaller pole toward the distal sulcus.

Size.—Various species range in total length (bladder tip to bladder tip) from as small as 40 to over 100 microns.

Ornamentation.—External bladder surface minutely granulose or rugose; internally the bladders are usually at least weakly reticulate. Proximal cap may be nearly smooth, rugose or striate. Distal body wall least ornamented.

Haptotypic features.—Lacking or nearly so. Presumably a weak vestigial imprint of the trilete mark may be present on the proximal cap in some forms as it occasionally is in modern *Abies*.

Pollen coat.—The unique character of internal bladder wall reticulation distinguishes these and many other coniferous pollen grains. The internal reticulae add apparent thickness to the perineal bladder membrane which is quite thin. The exinal (body) wall is much thicker proximally and is least translucent, sometimes appearing brownish under the microscope; the distal wall is much thinner, serving as a harmomegathus and point of germinal exit when ruptured by the expanding gametophyte.

Affinity.—There can be little question that grains of this sort are referable to the Coniferae. Members of modern Podocarpaceae and Pinaceae show essentially similar features. Correlatives of species of *Pityosporites* represented by vegetative organs are hardly recognized in Paleozoic formations. The presence of such pollen is evidence that such plants existed, possibly as a xerophytic upland flora, and tend to substantiate the view long held that an important ancestry, very scantily represented among megascopic fossils, preceded those highly developed forms found better represented in younger strata.

Pityosporites represents a group of Coniferae whose pollen is essentially modern in aspect. Florin's brilliant researches (1938-1940) have sufficiently demonstrated that *Lebachia*, *Ernestiodendron*, and *Walchianthus* for the most part do not possess pollen of the *Pityosporites* type; most, if not all of the probably correlated but isolated pollen of this sort is referable to *Florinites* n. gen. described below (p. 56).

Remarks.—It will be evident that the interpretation given *Pityosporites* here differs from that of Florin. He (1940, pp. 327-8) considers *Pityosporites* to be a completely artificial genus which has no type species. Apparently he would assign any pollen-like form with two bladders to this group. It is evident from Seward's descriptions, however (1914, 1919, 1933), that the emphasis is not so much merely on the presence of two bladders as it is on the essentially modern

aspects of these fossils which have been more precisely itemized in our revised definition.⁷ A more restricted group is thus indicated than that considered by Florin, and this group surely is not an artificial one although it certainly exceeds the scope of most "normal" genera, and, in fact, possibly contains elements which would be classed in separate families if more complete characterization could be obtained. Nevertheless, we think it necessary to treat the group as a genus at present, with the hope that critical studies later will permit it to be subdivided into somewhat smaller groups that will more perfectly represent the relationships in detail. Whether this hope is a vain one cannot be foretold *a priori*, but the desirability of recognizing a type species for this group which, as we construe it, does signify a definite natural plant alliance, cannot be denied. Part of the taxonomist's responsibility is to place the systematic data in order so that later students may revise it to greater perfection in the light of additional data. Such progress is very difficult if nomenclatural types are not definitely indicated and fully utilized in the application of technical nomenclature. In paleobotanical studies it is particularly important that this be recognized because the nature of the material that is being studied rarely permits categorical statement and new discoveries call for greater revision in preexisting concepts, perhaps, than in any other plant science.

Pityosporites can hardly be considered as synonymous with any modern genus; perhaps the most important reason is that when pollen characters are sufficiently distinctive to permit actual identification with a more precisely delimited modern group, identification with the genus *Pityosporites* becomes inadequate as an expression of affinity. Quite evidently many of the isolated ancient pollen grains cannot be more definitely assigned and *Pityosporites* will serve a most useful function in these instances.

⁷ Although Seward (1919, pp. 398-9) has included one of the forms Nathorst reported from the Hor clay as "*Pityosporites* sp." (which we should prefer to assign to *Alisporites*), Seward apparently did this on the assumption that Nathorst's specimen was similar to pollen of *Picea excelsa*. Wodehouse (1935) has shown *Picea* pollen to be very different. The *Pityosporites* sp. of Solms from Franz Josef Land (Seward, 1919, p. 399) no doubt is correctly assigned.

In addition to the nine species listed below, Kosanke (1943) also has recorded material of this nature from the Upper Pennsylvanian of Ohio.

1. PITYOSPORITES ANTARCTICUS Seward, 1914, Nat. Hist., Report British Antarctic (Terra Nova) Exped. 1910. Geology vol. 1, no. 1, pp. 23-4, pl. 8, fig. 45.
Pityosporites antarcticus Seward, 1919, Fossil Plants, vol. IV, p. 398.
Pityosporites antarcticus Seward, 1933, New Phyt., vol. 32, no. 4, pp. 311-313, fig. 1. Age, "Not older than Lower Mesozoic."
2. PITYOSPORITES CHINLEANA Daugherty, 1941, Carnegie Inst. Washington, Pub. 526, p. 398, pl. 34, fig. 5.
Age, Upper Triassic.
3. PITYOSPORITES (?) JEFFREYI Florin, 1940, Paleontographica vol. 85, Abt. B, no. 5, p. 327, pl. 163-4, figs. 8-12.
Pityanthus jeffreyi Florin (nomen nudum?), 1927, Arkiv. för Botanik, vol. 21A, no. 13, p. 6. (Systematic status of this nomenclatural combination is difficult to decide, since illustrations needed to validate it were not published till 1940 when the species was transferred to *Pityosporites*.)
Age, Middle Stephanian.
Note.—Bladders are seemingly set nearly opposite though it is possible their distal inclination merely is not apparent in the figures. The proximal cap also is not evident and it may be this form belongs to *Alisporites* rather than in the present genus.
4. PITYOSPORITES PALLIDUS Reissinger (nomen nudum), 1939, Paleontographica, vol. 84, Abt. B, p. 14.
Age, Lowest Jura (Lias).
Note.—An illustration required to validate the name has not yet been published.
5. PITYOSPORITES SEWARDI Virkki, 1937, Indian Acad. Sci. Proc., vol. 6, no. 6, sect. B, pp. 428-431, figs. 2a, b, c, d, pl. 32, figs. 1a, b, c.
Age, Lower Gondwana, above Talchir boulder bed.
6. PITYOSPORITES STEPHANENSIS Florin, 1940, Paleontographica, vol. 85, Abt. B, no. 5, pp. 327-8, pl. 163-4, figs. 13-16.
Age, Middle Stephanian.
7. PITYOSPORITES sp. Florin, 1940, idem, p. 61, pl. 163-4 fig. 17, fig. 18?
Age, Lower Rothliegendes.
Note.—No inclination of bladders shown.
8. PITYOSPORITES (?) sp. Florin, 1940, idem, p. 62, pls. 165-6, fig. 20.
Age, Upper Carboniferous.
Note.—No inclination of bladders shown.
9. PITYOSPORITES sp. Daugherty, 1941, Carnegie Inst. Wash., Pub. 526, description of pl. 34, figs. 7 and 8.
Age, Keuper.

Genus PUNCTATI-SPORITES (Ibrahim, 1933) emend., S. W. and B.,

Plate 1, figures 4-4b

Symmetry.—Spores radial, trilete.

Shape.—Originally nearly spherical, or possibly broadly rounded triangular with slight shortening of the axial dimension; when compressed the spores show no proximo-distal orientation preference.

Size.—Spores of various species range from 45 to 85 microns in mean diameter.

Ornamentation.—Various; surfaces levigate to punctate, rugose, reticulate or mildly apiculate.

Haptotypic structures.—Of moderate prominence, relative length of trilete rays highly variable between different species; no equatorial or arcuate markings (connecting ends of trilete rays) are present; lips of the trilete commissure are never very prominent nor highly ornamented.

Spore coat.—Generally thin, and, except in instances where ornamental features are most prominent, hardly in excess of 3 microns.

Affinity.—Spores of this genus are similar to those obtained from certain pteridospermic fructifications and from some fossils assigned to the ferns. The spores Kidston (1906) obtained from various *Crossotheca* fructifications are characteristic of typical species of *Punctatisporites*. However, many of the species represented by isolated spores have no known pteridospermic relationship although there is no adequate basis for separating them from forms which are thus allied. Much remains to be discovered as to the affinities of this genus, which is a rather large one, and it may be expected that some diverse elements have been included which will be segregated on the basis of newer information. It is quite possible that some of the forms assigned to *Punctatisporites* are merely immature and lack their distinctive mature ornamentation. Such may be the case for immature forms that in reality belong to *Raistrickia* n. gen. described below (p. 55). Immature forms should not be arbitrarily assigned to *Punctatisporites* but it is well to recognize that when these are present in substantial numbers, they need to be reported and that a superficial resemblance to

Punctati-sporites may not always be indicative of relationship. The affinity of certain of the species with the *Crossotheca* alliance of pteridosperms seems beyond much question, however.

The forms which Raistrick (1933, 1934, 1937) has assigned to his types B₅, B₆, D₃, D₆, D₁₅ (Knox, 1938), E₅, E₆, E₇, E₈, F₉, F₇, F₈ (Knox, 1938) (also 1K (?), 2K and 7K, Knox, 1942) appear entirely or in part referable to *Punctati-sporites*. It also may include some of the forms he has classed as B₃ and B₆. Some difficulty is encountered because Raistrick evidently has designated no single typical example for these groups and his illustrations of the forms have differed for individual types beyond what may represent a specific range of variability. Thus there may be some question as to the consanguinity of forms labeled as D₃ (cf. also Raistrick, 1935). Figures and description of E₁ given in 1933 do not exactly correspond with that given in later papers (1934, 1935). Illustrations of B₃ given in 1933 seem to resemble *Punctati-sporites* but those illustrated in later papers without much doubt are referable to *Calamospora* n. gen. described below. Since Raistrick's procedure is non-taxonomic it is impossible to form more than a general opinion as to specific equivalences in most instances.

Remarks.—The genus *Punctati-sporites* as given here includes twenty-nine species, four of which are queried. All but three of these names (see spp. Nos. 9, 21, 22) are new combinations. The group *Punctati-sporites* was originally defined by Ibrahim (1933, p. 21) as including trilete type spores with a granular surface, characters which by themselves can hardly be accepted as diagnostic of any generic group. Three species were described, one of which, *P. punctatus*, was designated as the type. Consequently it has been possible to define the genus practically, only by segregating those forms which appeared congeneric with *P. punctatus*, and the emended generic diagnosis has been constructed on this basis. Neither of the other two species Ibrahim originally placed in the genus are considered closely enough related to remain there; *P. parvus* Ibrahim is now assigned to the genus *Granulati-sporites*, and *P. pallidus* (Loose) Ibrahim to *Calamospora* n. gen.

Six species previously assigned to *Verrucosi-sporites* Ibrahim, including the type, are here placed under *Punctati-sporites*. *Verrucosi-sporites* thus would more reasonably be taken as the designation for the genus except that in meaning one name is no more suitable than the other and strict interpretation of page priority (p. 21 vs. p. 25) favors *Punctati-sporites*. The genus also includes the type of *Apiculata-sporites* Ibrahim (1933), a monotypic genus which seems based entirely on Ibrahim's inability to observe the trilete sutures described by Loose (1932) on *Sporonites spinulistratus*. The presence of the trilete marking on this species was reaffirmed by Loose in 1934. In any event the genus *Apiculata-sporites* does not seem securely founded and its one species is here placed under *Punctati-sporites*. Both groups, *Verrucosi-sporites* Ibrahim and *Apiculata-sporites* Ibrahim, consequently are regarded as congeneric with and the names synonyms of *Punctati-sporites*.

The holotype of the type species, *Punctati-sporites punctatus* (Ibrahim) Ibrahim, is from the Aegir coal seam at the top of the Westphalian B in the Ruhr district of Western Germany.

1. PUNCTATI-SPORITES ACULEATUS (Ibrahim) S. W. and B., comb. nov.
Apiculati-sporites aculeatus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 23, pl. 6, fig. 57.
2. PUNCTATI-SPORITES AUREUS (Loose) S. W. and B., comb. nov.
Reticulati-sporites aureus Loose, 1934, Inst. Paleobot. Arb., vol. 4, no. 3, p. 155, pl. 7, fig. 24.
3. PUNCTATI-SPORITES (?) AURICULAERENS (Loose) S. W. and B., comb. nov.
Sporonites auriculaferens Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 450, pl. 18, fig. 39.
Valvisi-sporites auriculaferens (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 152.
4. PUNCTATI-SPORITES BUCCULENTUS (Loose) S. W. and B., comb. nov.
Verrucosi-sporites bucculentus Loose, 1934, idem, p. 154, pl. 7, fig. 15.
5. PUNCTATI-SPORITES CORRUGATUS (Ibrahim) S. W. and B., comb. nov.
Reticulati-sporites corrugatus Ibrahim, 1933, Sporenformen des Aegirhorizonts, pp. 35-36, pl. 5, fig. 41.

6. PUNCTATI-SPORITES CUSUS (Loose) S. W. and B., comb. nov.
Reticulati-sporites cusus Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 156, pl. 7, fig. 25.
7. PUNCTATI-SPORITES FIRMUS (Loose) S. W. and B., comb. nov.
Verrucosi-sporites firmus Loose, 1934, idem, p. 154, pl. 7, fig. 30.
8. PUNCTATI-SPORITES GLOBOSUS (Loose) S. W. and B., comb. nov.
Apiculati-sporites globosus Loose, 1934, idem, p. 152, pl. 7, fig. 14.
9. PUNCTATI-SPORITES GRANDIVERRUCOSUS Kosanke, 1943, Am. Midland Naturalist, vol. 29, no. 1, pp. 127, 128, pl. 3, fig. 4.
10. PUNCTATI-SPORITES GRANIFER (Ibrahim) S. W. and B., comb. nov.
Granulati-sporites granifer Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 22, pl. 8, fig. 72.
11. PUNCTATI-SPORITES GRUMOSUS (Ibrahim) S. W. and B., comb. nov.
Verrucosi-sporites grumosus Ibrahim, 1933, idem, p. 25, pl. 8, fig. 68.
12. PUNCTATI-SPORITES INSIGNITIS (Ibrahim) S. W. and B., comb. nov.
Apiculati-sporites insignitis Ibrahim, 1933, idem, p. 24, pl. 6, fig. 54.
13. PUNCTATI-SPORITES (?) IRREGULARIS (Berry) S. W. and B., comb. nov.
Zonales-sporites irregularis Berry, 1937, Am. Midland Naturalist, vol. 18, no. 1, p. 156, fig. 9.
14. PUNCTATI-SPORITES LACUNOSUS (Ibrahim) S. W. and B., comb. nov.
Reticulati-sporites lacunosus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 36, pl. 6, fig. 50.
15. PUNCTATI-SPORITES LATIGRANIFER (Loose) S. W. and B., comb. nov.
Sporonites latigranifer Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 452, pl. 19, fig. 54.
Granulati-sporites latigranifer (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 147.
16. PUNCTATI-SPORITES MACULATUS (Ibrahim) S. W. and B., comb. nov.
Reticulati-sporites maculatus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 36, pl. 6, fig. 56.
17. PUNCTATI-SPORITES MICROTUBEROSUS (Loose) S. W. and B., comb. nov.
Sporonites microtuberous Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 450, pl. 18, fig. 33.
18. PUNCTATI-SPORITES MICROVERRUCOSUS (Ibrahim), S. W. and B., comb. nov.
Verrucosi-sporites microverrucosus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 25, pl. 7, fig. 60.
19. PUNCTATI-SPORITES NOBILIS (Wicher) S. W. and B., comb. nov.
Sporites nobilis Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 186, pl. 8, fig. 30.
20. PUNCTATI-SPORITES PAPILLOSUS (Ibrahim) S. W. and B., comb. nov.
Verrucosi-sporites papillous Ibrahim, 1933, Sporenformen des Aegirhorizonts, pl. 5, fig. 44.
21. PUNCTATI-SPORITES PARVIPUNCTATUS Kosanke, 1943, Am. Midland Naturalist, vol. 29, no. 1, p. 127, pl. 3, figs. 3, 3a, 3b.
22. PUNCTATI-SPORITES PUNCTATUS (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 21, pl. 2, fig. 18.
Sporonites punctatus Ibrahim, 1932, Neues Jahrb., Beilage-Band 57, Abt. B, p. 448, pl. 15, fig. 18.
Punctati-sporites punctatus (Ibrahim) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 146, pl. 7, fig. 27.
23. PUNCTATI-SPORITES (?) RETICULOCINGULUM (Loose) S. W. and B., comb. nov.
Sporonites reticulocingulum Loose, 1932, Neues Jahrb., Beilage-Band 57, Abt. B, p. 450, pl. 18, fig. 41.
Reticulati-sporites reticulocingulum (Loose) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 34.
Reticulati-sporites reticulocingulum (Loose) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 156.
24. PUNCTATI - SPORITES SPAHEROTRIANGULATUS (Loose) S. W. and B., comb. nov.
Sporonites sphaerotriangulatus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 451, pl. 18, fig. 45.
Laevigati-sporites sphaerotriangulatus (Loose) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 20.
Laevigati-sporites sphaerotriangulatus (Loose) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 145.
25. PUNCTATI-SPORITES SPINOSUS (Loose) S. W. and B., comb. nov.
Apiculati-sporites spinosus Loose, 1934, idem, p. 153, pl. 7, fig. 20.
26. PUNCTATI-SPORITES SPINULISTRATUS (Loose) S. W. and B., comb. nov.
Sporonites spinulistratus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 451, pl. 18, fig. 47.

- Apiculata-sporites spinulistratus* (Loose)
Ibrahim, 1933, Sporenformen des Aegir-horizonts, p. 37.
- Apiculati-sporites spinulistratus* (Loose)
Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 153.
27. PUNCTATI - SPORITES TRIGONORETICULATUS
(Loose) S. W. and B., comb. nov.
Reticulati - sporites trigonoreticulatus
Loose, 1934, idem, p. 155, pl. 7, fig. 9.
28. PUNCTATI-SPORITES (?) VELATUS (Loose)
S. W. and B., comb. nov.
Reticulati-sporites velatus Loose, 1934,
idem, p. 155, pl. 7, fig. 19.
29. PUNCTATI-SPORITES VERRUCOSUS (Ibrahim)
S. W. and B., comb. nov.
Sporonites verrucosus Ibrahim, 1932,
Neues Jahrb., Beilage-Band 67, Abt. B, p.
448, pl. 15, fig. 17.
Verrucosi-sporites verrucosus (Ibrahim)
Ibrahim, 1933, Sporenformen des Aegir-horizonts, p. 25, pl. 2, fig. 17.

Genus GRANULATI-SPORITES (Ibrahim,
1933) emend., S. W. and B.

Plate 1, figures 8-8b

Symmetry.—Spores radial, trilete.

Shape.—Originally oblate, rounded triangular, with the axial dimension much the shortest; when compressed the spores are nearly always flattened in good proximo-distal orientation since the transverse plane of the spore, being broadest, tends to parallel the bedding of sediments enclosing them. When preserved thus, the spores appear subtriangular in outline, with sides either convex or slightly concave and the corners rounded.

Size.—Spores of various species range from about 25 to 45 microns in mean diameter.

Ornamentation.—Various, surfaces smooth to punctate, finely to relatively coarsely reticulate or apiculate; the diverse types of ornamentation which characterize various species are not prominent to the extent that they mask the essential shape characteristics of the spores.

Haptotypic structures.—Trilete rays are well extended toward the corners; they are never relatively short. The lips are not distinguished by special ornamentation, the commissure is relatively simple but definite in all cases; usually no variations in ornamentation distinguish the proximal (pyramic) side from the rest of the spore coat.

Spore coat.—Of relatively uniform thickness throughout, generally thin, and except where modified by ornamentation, often less than 2 microns.

Affinity.—Spores similar to those of *Granulati-sporites* have been reported from fructifications of ferns although relatively few of these have been critically described. Spores of *Boweria minor* and *Renaulitia gracilis* which are illustrated by Knox (1938) are of similar character. Probably considerable difficulty will be encountered in definitely correlating the genus (further emended as may prove desirable) with any single supra-generic plant group. The many similar features possessed by species assigned to *Granulati-sporites* suggest that this grouping may be a practical one.

The forms Raistrick (1933, 1934, 1937) designates as D_4 , D_8 and D_{14} (Knox, 1938) probably belong to *Granulati-sporites* as defined here. Likewise Millott's Type 4 is of this character (Millot, 1939).

Remarks: The genus as emended includes fifteen species, twelve of which represent new name combinations. The genus was originally established to include spores of trilete-type showing granular sculpturing (Ibrahim, 1933, p. 21), characters which in themselves are inadequate; consequently it must be regarded as coincidence that two of the three original species (one of which was designated as the type) are retained in the group, along with another that Loose assigned to it in 1934. The genotype of *Granulati-sporites* is the only genotype species included by revision within the genus and thus there can be no question as to validity of the generic name. The genotype, *G. granulatus* Ibrahim, also is based on a form from the Aegir coal bed at the top of the Westphalian B.

1. GRANULATI-SPORITES DELTIFORMIS S. W. and B., nomen nov.

Triquitrites deltoides Wilson and Coe,
1940, Am. Midland Naturalist, vol. 23, no.
1, p. 185, fig. 9.

Note.—In combination with *Granulati-sporites* the specific epithet becomes a homonym of *G. deltoides* (Ib.) S. W. and B., as given below.

2. GRANULATI-SPORITES DELTOIDES (Ibrahim)
S. W. and B., comb. nov.

Sporonites deltoides Ibrahim, 1932,
Neues Jahrb., Beilage-Band 67, Abt. B, p.
448, pl. 15, fig. 15.

Laevigati-sporites deltoides (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 20, pl. 2, fig. 2.

Note.—The species is larger than most forms assigned to *Granulati-sporites*.

3. GRANULATI-SPORITES FISTULOSUS (Ibrahim) S. W. and B., comb. nov.

Reticulati-sporites fistulosus Ibrahim, 1933, idem, p. 36, pl. 5, fig. 35.

4. GRANULATI-SPORITES GIBBOSUS (Ibrahim) S. W. and B., comb. nov.

Verrucosi-sporites gibbosus Ibrahim, 1933, idem, p. 25, pl. 6, fig. 49.

5. GRANULATI-SPORITES GRANULATUS Ibrahim, 1933, idem, p. 22, pl. 6, fig. 51.

Note.—Type species of *Granulati-sporites*.

6. GRANULATI-SPORITES MICROGRANIFER Ibrahim, 1933, idem, p. 22, pl. 5, fig. 32.

7. GRANULATI-SPORITES MICROSACETOSUS (Loose) S. W. and B., comb. nov.

Sporonites microsactosus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 450, pl. 18, fig. 40.

Setosi-sporites microsactosus (Loose) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 26.

Setosi-sporites microsactosus (Loose) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 148.

8. GRANULATI-SPORITES MICROSPINOSUS (Ibrahim) S. W. and B., comb. nov.

Apiculati-sporites microspinosa Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 24, pl. 6, fig. 52.

9. GRANULATI-SPORITES PARVUS (Ibrahim) S. W. and B., comb. nov.

Sporonites parvus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 448, pl. 15, fig. 21.

Punctati-sporites parvus (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 21, pl. 2, fig. 21.

Reticulati-sporites parvus (Ibrahim) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 154, pl. 7, fig. 13.

10. GRANULATI-SPORITES PIROFORMIS Loose, 1934, idem, vol. 4, no. 3, p. 147, pl. 7, fig. 19.

11. GRANULATI-SPORITES (?) PRIDDYI (Berry) S. W. and B., comb. nov.

Zonales-sporites priddyi Berry, 1937, Am. Midland Naturalist, vol. 18, no. 1, p. 156, fig. 2.

12. GRANULATI-SPORITES TORQUIFER (Loose) S. W. and B., comb. nov.

Sporonites torquifer Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 450, pl. 18, fig. 43.

Reticulati-sporites torquifer (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 154.

13. GRANULATI-SPORITES TRIGONUS (Ibrahim) S. W. and B., comb. nov.

Reticulati-sporites trigonus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 37, pl. 5, fig. 34.

14. GRANULATI-SPORITES TRIQUETRIS (Ibrahim) S. W. and B., comb. nov.

Verrucosi-sporites triquetris Ibrahim, 1933, idem, p. 26, fig. 61.

15. GRANULATI-SPORITES VERRUCOSUS (Wilson and Coe) S. W. and B., comb. nov.

Triquetrites verrucosus Wilson and Coe, 1940, Am. Midland Naturalist, vol. 23, no. 1, p. 185, fig. 10.

Genus ALATI-SPORITES Ibrahim, 1933

Plate 1, figures 6-6b

Symmetry.—Spores radial, trilete.

Shape.—Body, exclusive of bladders, is sub-triangular.

Size.—In the vicinity of 80 microns, overall diameter.

Ornamentation of spore.—Body moderate; may be punctate, finely reticulate; bladders smooth to punctate, etc. Bladders, in general, less definitely ornamented than spore body.

Haptotypic structures.—Trilete rays relatively long, little ornamented.

Spore coat.—Consisting of two distinct membranes; the outer (perisporal) membrane is very thin and expanded in the inter-radial areas to form bladders in a trimorous (in threes or multiples of three) pattern. The spore body wall (exospore) is usually more than twice as thick as the bladder membrane, darker, and easily distinguished on that account.

Affinity.—Spores of *Alati-sporites* seem smaller but essentially similar in construction to those of *Spencerites* (Scott, 1898, Kubart, 1910). The three interradial bladders are most distinctive in both genera. The significance of this character is hardly well enough understood to properly evaluate evidence as to their relationship.⁸

⁸ The haptotypic relations, if any, of the three bladders present on pollen of *Podocarpus dacrydioides* and on *Pherosphaera* are not known, and comparison with Carboniferous forms does not seem particularly pertinent for obvious reasons.

It seems doubtful that the form described by Daugherty (1941, p. 64) as *Spencerites? chinleana* is actually referable to *Spencerites* or could be referred to *Alati-sporites* since it apparently does not possess three interradial bladders. Daugherty does not mention and the figure given does not show the trilete sutures. If these were present the species might be referred to *Cirratiradites* provided the equatorial appendage was a flange. Lacking these characteristics, his alternative suggestion of a gymnospermic affinity seems most plausible.

Spores assigned by Raistrick to type D₅ without much question belong to *Alati-sporites*.

Remarks.—Only one species has been described to date but there is little doubt the group will receive far more recognition. It is highly distinctive and complex enough that specific characters are easily distinguishable. No doubt the character of the bladders will lend itself to the purpose. There is no possibility of these forms being confused with unseparated tetrad groups belonging to other genera although illustrations which have been published might lead one to think so.

In addition to its recognition in the Ruhr district and in Britain the genus has been recognized in coals of the Illinois basin by Brokaw and in Tennessee coals by Bentall. These from America appear to be specifically distinct and as yet undescribed forms.

The generic diagnosis given above has been constructed in the light of this additional information, and while considerably augmented over Ibrahim's meager description (1933, p. 32), it may be improper to consider it as a generic emendation. The type, of course, is the species given below, which was first described from the Aegir coal in the Ruhr.

1. *ALATI - SPORITES PUSTULATUS* (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 33, pl. 1, fig. 12.

Sporonites pustulatus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 448, pl. 14, fig. 12.

Alati - sporites pustulatus (Ibrahim) Ibrahim, Loosse, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 151, pl. 7, fig. 4.

Type D₅ Raistrick, 1937, Congrès pour l'avancement des études de stratigraphie carbonifère, Heerlen, 1935, Compte rendu, vol. 2, p. 911.

Genus *RETICULATI-SPORITES* (Ibrahim, 1933) emend., S. W. and B.

Plate 1, figures 7-7b

Symmetry.—Spores, in essence, radially symmetrical; some species are weakly trilete and others show no indication of their tetrahedral tetrad origin but are considered trilete in derivation because of their shape.

Shape.—Originally spherical or moderately oblate; compressed spores are circular disk-like, generally without prominent folds.

Size.—Spores of various species range from about 40 to 100 microns in diameter.

Ornamentation.—Coarsely and often irregularly reticulate; aside from the coarse ornamentation the body wall may have a variously smooth, punctate or finely reticulate texture. In the "alete" forms reticulation may show a tendency toward a spiral pattern; in others it may be mostly limited to the distal part of the spore.

Haptotypic structures.—The trilete structures may be weakly developed; no arcuate ridges are developed but the ornamentation may sometimes be absent on the proximal surface. The trilete rays vary considerably in development and length among different species.

Spore coat.—Appears to consist oftentimes of two membranes; when present, the outer one (perisporal?) is thinner and more or less intimately connected with the coarse reticulation; the inner (exosporal?) membrane is thicker and sometimes irregular and excentric in its development. The wall may appear thick, and yet be quite translucent.

Affinities.—The only spores of this general or possible character known in fructifications are allied with *Sphenophyllum*. *Sphenophyllum* spores are inadequately known in the detail necessary for close comparison, however, and considerably more evidence is needed to form an opinion as to the relationship of *Reticulati-sporites* with other groups.

Types C₂, C₃, F₄, and F₆ of Raistrick (1934, 1935, 1937) and possibly also F₁, F₂ (cf. Knox, 1938), F₃ and F₄, appear to belong to *Reticulati-sporites*. Types F₅ and F₆ and D₁₃ (Knox, 1938) are more problematic. Type 8 of Millott (1939) also belongs here and is most closely related to *R. facetus* of species now described. Knox' Type 5K may possibly be similar to some species included in *Reticulati-sporites*. Spores illustrated by Knox (1939) from Fifeshire, figs. 49 and 50, unquestionably belong to *Reticulati-sporites*. Unpublished forms of similar nature have been found in Ohio coals by Wilson and Brokaw, and they have also been recognized in Iowa and Illinois and Tennessee.

Remarks.—Seven species are included here under *Reticulati-sporites*, only one of which represents a new name combina-

tion. This form, *R. facetus* (Ibrahim), was originally designated as the genotype of *Reticulata-sporites* with five species assigned to it. Essentially the only character shared by these five was their lack of a visible haptotypic marking. Most diverse types of reticulation characterized their surfaces. *R. facetus*, however, shows a type of reticulation which is very similar to that of *R. reticulatus* (genotype of *Reticulati-sporites*) and others in this genus. Other characters are also in substantial agreement and it is believed that the lack of a trilete marking in this case is insufficient basis for generic separation. Other species of *Reticulati-sporites* show a very weak trilete marking. Consequently *Reticulata-sporites* Ibrahim (1933, p. 38) may be dispensed with and regarded as a later synonym for *Reticulati-sporites* Ibrahim (1933, p. 33).

Knox (1939) has suggested that aleo spores with somewhat spiral reticulation such as shown by *R. facetus* (cf. fig. 49) resemble spores of *Riccia* but this comparison does not seem particularly close. Neither does the comparison of the *R. corporeous* type with *Fossombronia* spores seem appropriate because the fossil forms evidently have a perisporal membrane enclosing them instead of mere "large alveolae with high lamellae." Nevertheless it must be admitted that in general spores of *Reticulati-sporites* bear more resemblance to some of the spores of the Hepaticae illustrated by Knox than any of the other Paleozoic groups. The apparent absence of haptotypic markings on several of the modern forms is a striking feature which should be more thoroughly investigated, although it need not occasion great surprise to find so advanced a character in a group whose discrete phylogeny goes back at least to the Carboniferous.

It may be suggested that spores of *Reticulati-sporites* underwent more modification within the sporangium subsequent to the breakup of the original tetrad than is usual for cryptogamic spores. The highly developed reticulation pattern probably was laid down relatively late in sporogenesis by a tapetal plasmodium, sometimes without respect for the proximo-distal relationships established in original tetrad groupings. Such a sequence occurs in formation of many kinds of angiospermic pollen. Spores of *Reticulati-*

sporites apparently lack the further specialization of germinal pores, nevertheless lack of good development of a trilete commissure in some of the forms might possibly signify that the plants represented here had passed beyond the typical cryptogamic stage of evolution. *Reticulati-sporites* appears to be a relatively homogeneous group of natural relationship. The coarse reticulation is highly characteristic and for the most part quite unmistakable. Nevertheless these forms are rather anomalous in their morphology and offer difficulties in interpretation. Those suggested are regarded as tentative only.

The genus is best known from the Aegir coal bed at the top of the Westphalian B, which is approximately equivalent in age to middle Des Moines and upper Pottsville-lower Allegheny beds.

1. RETICULATI-SPORITES CORPOREUS Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 155, pl. 7, fig. 7.
2. RETICULATI-SPORITES FACETUS (Ibrahim) S. W. and B., comb. nov.
Reticulata-sporites facetus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 38, pl. 5, fig. 36.
3. RETICULATI-SPORITES MEDIARETICULATUS Ibrahim, 1933, idem, p. 34, pl. 7, fig. 62.
4. RETICULATI-SPORITES ORNATUS (Ibrahim) Ibrahim, 1933, idem, p. 35, pl. 1, fig. 7.
Sporonites ornatus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 447, pl. 14, fig. 7.
5. RETICULATI-SPORITES POLYGONALIS (Ibrahim) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 155, pl. 7, fig. 16.
Sporonites polygonalis Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 447, pl. 14, fig. 8.
Laevigati-sporites polygonalis (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 19, pl. 1, fig. 8.
6. RETICULATI-SPORITES RETICULATUS (Ibrahim) Ibrahim, 1933, idem, pp. 33-34, pl. 1, fig. 3.
Sporonites reticulatus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 447, pl. 14, fig. 3.
Reticulati-sporites reticulatus (Ibrahim) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 156.
- Note.—Type species of *Reticulati-sporites*.
7. RETICULATI-SPORITES (?) RETICULIFORMIS Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 34, pl. 7, fig. 63.
Note.—Trilete rays are unusually long and well developed in this species.

NOMINA EXCLUDENDE

1. RETICULATI-SPORITES ANGULATUS Ibrahim, 1933, Sporenformen des Aegirhorizonts, etc., p. 35, pl. 7, fig. 59.
2. RETICULATI-SPORITES BIRETICULATUS (Ibrahim) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 158, pl. 7, fig. 28.
Sporonites bireticulatus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 447, pl. 14, fig. 1.
Reticulati-sporites bireticulatus (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, etc., p. 35, pl. 1, fig. 1.
3. RETICULATI-SPORITES FACIERUGOSUS Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 155, pl. 7, fig. 26.
4. RETICULATI-SPORITES MEDIAPIUDENS Loose, 1934, idem, p. 158, pl. 7, fig. 8.
5. RETICULATI - SPORITES MICRORETECULATUS (Loose) Loose, 1934, idem, p. 155.
Sporonites microreticulatus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 450, fig. 37.
6. RETICULATI-SPORITES MOROSUS Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 154, pl. 7, fig. 2.
7. RETICULATI-SPORITES NEXUS (Loose), Ibrahim, 1933, Sporenformen des Aegirhorizonts, etc., p. 34.
Sporonites nexus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 450, fig. 35.
Reticulati-sporites nexus (Loose) Ibrahim, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 156, pl. 18, fig. 35.
8. RETICULATI-SPORITES SIFATI Ibrahim, 1933, Sporenformen des Aegirhorizonts, etc., p. 35, pl. 8, fig. 67.
9. RETICULATI-SPORITES SPONGIOSUS Ibrahim, 1933, idem, p. 39, pl. 8, fig. 71.
10. RETICULATI-SPORITES VINCULATUS (Ibrahim), Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 156.
Sporonites vinculatus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 448, pl. 15, fig. 19.
Reticulata-sporites vinculatus (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, etc., p. 39, pl. 2, fig. 19.

Genus LAEVIGATO-SPORITES (Ibrahim, 1933) emend., S. W. and B.

Plate 1, figures 5-5b

Symmetry.—Spores bilateral, monolete.

Shape.—Originally broadly bean-shaped; elongate oval in the plane of longitudinal symmetry, round or oval in the transverse plane. When compressed the spores tend to be folded variously depending on the size and morphology of the various specific types of spores.

Size.—Spores of various species range from about 20 to over 130 microns in their long dimension.

Ornamentation.—Smooth to finely punctate, apiculate or rugose; rarely showing pronounced reticulation or strong apiculae.

Haptotypic structures.—Consisting of a simple monolete linear suture, generally without lips specially distinguished, and usually continued for more than half the total length of the spore. The suture may be very inconspicuous if it coincides in position with the edge of a compressed spore, or with the axis of a longitudinal fold. Ends of very delicate arcuate ridges

are sometimes distinguishable flaring laterally from both ends of the suture line.

Spore coat.—Varying somewhat in thickness relative to the other dimensions; the spore coat is oftentimes thin and translucent. The internal cavity is sometimes more "bean-shaped" than the external outline due to internal thickening of the spore coat in the central proximal region.

Affinity.—Smaller species of *Laevigato-sporites* agree with some forms obtained from filicinean type fructifications. There is now no particularly good evidence as to the affinity of the larger forms. Fredda Reed (1938, p. 333) has obtained spores of this type from an extraordinary new type of Calamarian fructification which are approximately 50 microns in length. Spores of *Zeilleria* are of this type (Florin, 1937, p. 316-7) but it is not now possible to decide whether that genus belongs to the ferns or pteridosperms (Halle, 1933, p. 88). The "distal furrow" of *Zeilleria* spores remarked by Florin (1937, p. 317) appears no more definite than many of the fortuitous folds seen in spores of *Laevigato-sporites*.

It thus appears that species of *Laevigato-sporites* could conceivably pertain to at least three distinct contemporaneous orders of Paleozoic plants. It seems doubtful that our information on these relationships will be greatly improved in the immediate future and until it is possible to revise the genus on the basis of reliable evidence it will serve a useful geological, if not a botanical, purpose. In a good many instances species of *Laevigato-sporites* form a majority of the spores obtained from certain coal beds. They are, however, rare or absent in a number of lower Pottsville coals that have been examined.

Spores evidently belonging to *Laevigato-sporites* have been assigned to types B₁a, B₁b, and B₈ by Raistrick (1933, 1937) (Knox, 1938). Millott's types 6 and E₂a (Millott 1939) and Knox' (1942) Type 6K may also belong here.

Remarks.—Nine species, one of which includes three designated *formae*, are now listed for *Laevigato-sporites*. Ibrahim originally assigned two species to the genus. The second of these, *L. ellipsoidea*, is now referred to *Monoletes*. It is pos-

sible that some of the names given below will prove to be synonyms. On the other hand a number of distinct and as yet unrecorded species have been recognized in the Illinois basin and elsewhere.

The list includes genotype species of four previously named genera. *L. bilateralis* (Loose) was the only species described by Loose (1934, p. 159) under the new name, *Reticulato-sporites*. The name was credited to "Ibrahim 1932" although no "reticulate" was ever used by that author. *L. desmoinensis* is the genotype of *Phaseolites* Wilson and Coe (1940). *L. minutus* (Ibrahim) was the sole species given under *Punctato-sporites* by Ibrahim (1933, p. 40). *L. vulgaris* Ibrahim is the designated genotype of *Laevigato-sporites* Ibrahim (1933, p. 39). All of these species are evidently congeneric, their chief distinction being in variation of surface ornament and small differences of size, none of which can be regarded as of more than specific importance. The names *Reticulato-sporites*, *Phaseolites*, and *Punctato-sporites* are therefore regarded as synonyms of *Laevigato-sporites*. All these are typically represented by specimens from the upper part of the Westphalian B and approximately equivalent beds in America.

1. LAEVIGATO-SPORITES BILATERALIS (Loose), S. W. and B., comb. nov.

Reticulato-sporites bilateralis Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 159, pl. 7, fig. 22.

Note.—*Reticulato-sporites* is a generic name published only by Loose (1934) although he erroneously credited it to "Ibrahim, 1932."

2. LAEVIGATO-SPORITES CRANMORENSIS Berry, 1937, Am. Midland Naturalist, vol. 18, no. 1, p. 157, fig. 1.

3. LAEVIGATO-SPORITES DESMOINENSIS (Wilson and Coe) S. W. and B., comb. nov.

Phaseolites desmoinensis Wilson and Coe, 1940, idem, vol. 23, no. 1, p. 183, fig. 4.

Note.—Evidently closely related to *Laevigato-sporites vulgaris*.

4. LAEVIGATO-SPORITES MINIMUS (Wilson and Coe) S. W. and B., comb. nov.

Phaseolites minimus Wilson and Coe, 1940, idem, vol. 23, no. 1, p. 183, fig. 5.

5. LAEVIGATO-SPORITES MINUTUS (Ibrahim) S. W. and B. comb. nov.

Punctato-sporites minutus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 40, pl. 5, fig. 33.

6. LAEVIGATO-SPORITES (?) PENNOVALIS Berry, 1937, Am. Midland Naturalist, vol. 18, no. 1, pp. 156-7, fig. 4.

7. LAEVIGATO-SPORITES THIESSENII Kosanke, 1943, Am. Midland Naturalist, vol. 29, no. 1, p. 125, pl. 3, figs. 1, 1a, 1b.

Pittsburgh microspore of Thiessen, various publications. See especially Thiessen and Staud, 1923.

8. LAEVIGATO-SPORITES (?) TUBERCULATUS (Berry), S. W. and B., comb. nov.

Tuberculati-sporites tuberculatus Berry, 1937, idem, vol. 18, no. 1, p. 155, fig. 9.

9. LAEVIGATO-SPORITES VULGARIS (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, pp. 39-40, pl. 2, fig. 16; pl. 5, figs. 37, 38, 39.

Sporonites vulgaris Ibrahim, 1932, Neues Jahrb. Beilage-Band 67, Abt. B, p. 448, pl. 15, fig. 16.

LAEVIGATO-SPORITES VULGARIS forma MINOR Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 158, pl. 7, fig. 12.

LAEVIGATO-SPORITES VULGARIS forma MAIOR Loose, 1934, idem, p. 158, pl. 7, fig. 6.

LAEVIGATO-SPORITES VULGARIS forma MAXIMUS Loose, 1934, idem, p. 158, pl. 7, fig. 11.

NOMEN EXCLUDENDE

1. LAEVIGATO-SPORITES RHEAENSIS Berry, 1937, Am. Midland Naturalist, vol. 18, no. 1, p. 157, fig. 13.

Note.—The morphology of this form is so obscure that its significance cannot be ascertained.

Genus ZONALO-SPORITES Ibrahim, 1933

Symmetry.—Spores apparently bilateral, monolete.

Shape.—Flattened elliptical (?), broadly elliptical in transverse plane.

Size.—Relatively large, 200-300 microns in length.

Ornamentation.—Surface smooth to minutely rugose.

Haptotypic features.—Linear proximal suture with slight angular median deflection, termini of arcuate ridges may be weakly differentiated.

Spore coat.—Perisporal bladder membrane thin, enveloping spore body on all sides, and in contact with it proximally and distally. Body wall (exospore) relatively thick and brownish translucent.

Affinity.—Probably pteridospermic, judging from points of similarity with *Monoletes* which is discussed later. It nevertheless is still extremely problematic since it superficially seems to combine features of spores of Medullosan and of Cordaitian relationship.

Remarks.—This genus is reported in only two instances, in the Ruhr and in Illinois, in both cases from relatively few specimens. The forms have been assigned to different species as listed below. Much more information is needed before their significance can be understood.

1. ZONALO-SPORITES AUREOLUS (Schopf) S. W. and B., comb. nov.
Monoletes aureolus Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, pp. 45-46, pl. 1, figs. 1-2.
2. ZONALO-SPORITES VITTATUS Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 41, pl. 6, fig. 45.

Genus MONOLETES (Ibrahim) 1933,
emend, S. W. and B.

Plate 2, figures 17-17c

Symmetry.—Spores apparently bilateral, monolete. Mature forms evidently have been modified considerably in post tetrad maturation, and it is possible that although the mature forms appear very definitely bilateral, they may have arisen from tetrahedral tetrads.

Shape.—Elliptical to rounded lenticular in outline as viewed from the proximal side; of similar figure but of more slender proportions in the plane of the long axis viewed from the side; the short transverse axis shows a somewhat rounder and shorter but notably flattened outline. The distal surface oftentimes is marked by two prominent grooves extending nearly the length of the spore with a well rounded umbo between. Sometimes the proximal side near the suture shows a very slight prominence. On compression, longitudinal folds frequently parallel the distal grooves.

Size.—Spores relatively large, varying from slightly over 100 microns to as much as half a millimeter in length.

Ornamentation.—Surfaces generally minutely granulose appearing quite smooth at low magnification; sometimes glistening in reflected light. Emphytic marking is evenly distributed except at the extreme base of distal grooves, which are more smooth.

Haptotypic features.—When closed the proximal suture is a very narrow linear groove, generally lacking marginal distinction, though the lip area may be very slightly upraised. The most noteworthy

and diagnostic feature is the slight angular deflection of the suture line near the middle. Although inconspicuous and sometimes hardly evident it seems to be universally present. It may constitute the sole remnant of a third vestigial ray in a fundamentally trilete suture pattern. Very weakly developed termini of arcuate ridges are occasionally resolved at the two ends of the functional suture line. The suture opens to form a sharp taper-pointed lenticular slit. The distal grooves have no connection with haptotypic structures.

Spore coat.—The exospore consists of a layer of varying thickness; the proximal side and the center of the distal umbo are as much as 15 or 18 microns; the thinnest is at the base of the distal grooves on either side of the umbo where it may be less than 5 microns. An even gradation exists between these extreme areas and in normally compressed spores the exospore thickness at the margin is intermediate between the extremes. The endosporal membrane is frequently evident as a crumpled translucent sack less than a micron in thickness, sometimes shrunken from the exospore at the spore margin. The umbo and distal grooves, when present, have the appearance of functioning as a harmomegathus.

Affinity.—Spores of this character distinguish a pteridospermic plant alliance probably largely coextensive with the Medullosaceae. They are characteristic of all genera placed in the Whittleseyinean sub-tribe (see Halle, 1933). The only aberrant feature is the lack of distal grooves in spores of *Codonotheca*; spores of all other genera now assigned to this alliance possess them. *Codonotheca* spores are otherwise entirely characteristic of *Monoletes* and when such spores are found isolated they probably should be assigned to *Monoletes* since there well may be other types in addition to *Codonotheca* that also may lack distal grooves and umbo. Spores of *Codonotheca* emphasize the non-essential character of these specialized distal structures.

Remarks.—Much of the previous discussion is based on comparative study of spores in *Dolerotheca* and *Codonotheca* by Schopf from petrified and compression material as well as from spores isolated by maceration of coal. It has thus been

possible to establish accurately from sections the proximal position of the suture and the distal location of the harmomegathic grooves. The fact that spores are frequently found with the suture opened but, except in instances of obvious mechanical or chemical injury, have never been observed with the umbo split off as an "operculum" or the grooves other than intact, strongly suggests that proximal gametophytic exit was still a fundamental feature of these forms as it must have been in their more ancient cryptogamic ancestry. Such spores are also regarded as prepollen (cf. Schopf, 1938, pp. 14-15).

The foregoing diagnosis serves to correct some erroneous interpretations of structure previously held; e.g. the "en-circling ridge" described by Schopf (1938, p. 45) for the species designated as *Monoletes ovatus*, is the margin of the distal grooves discussed here. It has no haptotypic significance although it possibly is not emphytic in origin in the same sense that ordinary surface ornamentation is.

Monoletes was first used by Ibrahim in 1933 to designate a new group in his artificial system. Although substantive in form and similar to a generic name, it was not originally applied in that sense and no nomenclatural type has been previously proposed. It has been used as a generic designation and applied more narrowly (Schopf, 1936, 1938); we now emend it to correspond with the restricted usage. *Monoletes ovatus* Schopf may serve as the type species of the genus. The group now includes two species, both of which appear to be widely distributed. It is likely that further species will be distinguished by application of more refined biometric procedure. Both species must still be regarded as rather generalized types.

1. MONOLETES ELLIPSOIDES (Ibrahim) Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, p. 45, pl. 1, fig. 14; pl. 6, figs. 5 and 6.

Sporonites ellipsoides Ibrahim, 1932, Neues Jahrb. Beilage-Band 67, Abt. B., p. 449, pl. 17, fig. 29.

Laevigato-sporites ellipsoides (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 40, pl. 4, fig. 29.

Punctato-sporites ellipsoides (Ibrahim) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, pp. 158-9, pl. 7, fig. 35.

Sporites ellipsoides (Ibrahim) Wicher, 1934, idem, vol. 4, no. 4, p. 185.

2. MONOLETES OVATUS Schopf, 1935, Illinois Acad. Sci. Trans. vol. 28, no. 2, p. 108, fig. 7. Pollen of *Dolerophyllum* sp., Zerndt, 1930, Acad. polonicae sci. Bull. internat., ser. B, pp. 55-56, pl. 8, figs. 42-49. Type 31 Zerndt, 1931, idem, ser. A, p. 176.

Monoletes ovatus Schopf, 1935, Illinois Acad. Sci. Trans. vol. 28, no. 2, p. 176.

Monoletes ovatus Schopf, 1938, Illinois Geol. Survey Rept. Inv. No. 50, pp. 43-45, pl. 1, figs. 3-5, pl. 6, figs. 1-4.

Pollen of *Dolerotheca fertilis*, Zerndt, 1940, Paleontographica, vol. 84, Abt. B, p. 136-138, pl. 11, fig. 36.

Genus DENSO-SPORITES (Berry, 1937), emend., S. W. and B.

Plate 1, figures 9-9c

Symmetry.—Spores radial, trilete.

Shape.—Originally oblate, round to subtriangular in equatorial outline. When compressed, the central area becomes much thinner than the margins due to variation in spore wall thickness. Coal thin sections, taken vertically through the coal bed, show them compressed into a "dumbbell" shape. The original highly oval sectional form results in extremely uniform proximo-distal orientation in enclosing sediments.

Size.—Diameter of specimens assigned among various species varies from about 35 to 100 microns.

Ornamentation.—Smooth to apiculate and rugose. External surface character typically is uniform, though ornamentation may be more strongly developed toward the equator in some forms.

Haptotypic structures.—A delicate trilete marking is visible in well preserved material or where the central area of the proximal surface is consistently present. "Fissures" penetrating to the margin in some instances may be essentially haptotypic continuations of the trilete sutures.

Spore coat.—Characterized by great differences in thickness. The proximal and distal walls are usually membranous, or at least significantly thinner than the equatorial portion of the coat. The latter area is oftentimes so thick it is practically opaque to transmitted light in contrast to the highly translucent central area. It may also be so extended centrifugally as to simulate a flange but it is not usually strictly demarcated from the spore body, as such.

Affinities.—Spores of this genus have not been recognized in connection with fructifications. This is surprising in view of their frequency in coal. They have been roughly designated as "biconcave," "salvershaped" and as "splint microspores" by Thiessen and his co-workers (Thiessen and Wilson, p. 9, 1924; Thiessen, 1930; Sprunk, et al, 1940) and can be recognized by their characteristic "dumbbell" shape in cross section.⁹

Modern methods of study may be expected therefore to disclose definite evidence of the relationship of this group. Their structure is so unusual that it seems evident that a single homogeneous group of plants for the most part is represented.

Raistrick's Type A spores (Raistrick and Simpson, 1933) apparently are nearly entirely referable to *Denso-sporites*. His A₅, A₆, (1934) and A₁₀ (1937, 1938) also are probably congeneric and, if so, appear to be the most bizarre of any in the genus. Possibly the A₃ spores (Raistrick, 1937; Knox, 1938) are least assuredly related to this group. Knox's Type C₆ (Knox, 1942) possibly might be placed here though its morphologic interpretation is somewhat uncertain due to its unusual type of equatorial development.

Remarks.—Six species are now included under *Denso-sporites* and it seems that a good many more will need be distinguished. Raistrick's A₅, A₆, and A₁₀ types are worthy of specific distinction. The generic name, while perhaps of undesirable construction, is not in conflict with any others that have been proposed and thus is entirely valid.

As mentioned previously, the spores are widespread and very abundant in splint coals. It has been suggested that a special type of vegetation was responsible for this type of coal but such can hardly be the case, since recognizable splint coals are also found that are so much younger that floral similarities cease (cf. Thiessen and Sprunk, 1936). White (in discussion of Thiessen, 1930, p. 672) doubts that the presence of a certain type of plants is responsible for forming this type of coal. The coincidence of occurrence between *Denso-sporites* and Paleozoic splint coal nevertheless seems unaccountably high and additional infor-

⁹ Thiessen has also designated some spores not referable to *Denso-sporites* as "splint spores."

mation about these spores may reflect importantly, although indirectly, upon the problem of splint coal formation.

1. DENSO-SPORITES ANNULATUS (Loose) S. W. and B., comb. nov.

Sporonites annulatus Loose, 1932, Neues Jahrb. Beilage-Band 67, Abt. B, p. 451, pl. 18, fig. 44.

Zonales-sporites annulatus (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 151.¹⁰

2. DENSO-SPORITES COVENSIS Berry, 1937, Am. Midland Naturalist, vol. 18, p. 157, fig. 11.

Note.—Although serving as genotype, the specific characteristics of this form are inadequately known.

3. DENSO-SPORITES DENSUS Berry, 1937, Am. Midland Naturalist, vol. 18, no. 1, pp. 157-8, fig. 7.

4. DENSO - SPORITES (?) INDIGNABUNDUS (Loose) S. W. and B., comb. nov.

Sporonites indignabundus Loose, 1932, Neues Jahrb. Beilage-Band 67, Abt. B, p. 451, pl. 19, fig. 51.

Zonales-sporites indignabundus (Loose) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 32.

Apiculatis-sporites indignabundus (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 153.

5. DENSO-SPORITES LORICATUS (Loose) S. W. and B., comb. nov.

Sporonites loricatus Loose, 1932, Neues Jahrb. Beilage-Band 67, Abt. B, p. 450, pl. 18, fig. 42.

Zonales-sporites loricatus (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 151.

6. DENSO-SPORITES (?) QUADRATUS Berry, 1937, Am. Midland Naturalist, vol. 18, p. 158, fig. 10.

Note.—A very problematic form.

Genus CYSTOSPORITES Schopf, 1938

Plate 1, figures 10-10b

Symmetry.—Spores radial, trilete.

Form and size.—Variable depending on development. Fertile members relatively enormous, sack-like, elongate, sometimes attaining a length of more than a centimeter and about half as broad. Abortive forms variable in development, characteristically ranging from as small as one-

¹⁰ Since Loose recognized the rather significant distinction between *Denso-sporites* and the zonate forms, in a footnote appended to his article he suggested "einer Unterabteilung *Annulatis-sporites*" for *D. annulatus* and *D. loricatus*. Because he did not adopt the name, "Unterabteilung *Annulatis-sporites*" is invalidly published, at least in the sense of a generic designation.

half a millimeter in diameter to more than twice that. Smallest forms are more nearly isodiametric becoming axially elongate with increased size. When compressed both abortive and fertile members are folded irregularly; their longest axis is generally least effected.

Ornamentation. — Generally absent; abortive forms may show apparent reticulation.

Haptotypic features. — Strongly developed in fertile forms but relatively inconspicuous because of the enormous expansion of the distal part of the spore body. Sutures definite, extended to the arcuate ridges which are strongly thickened, lips often moderately defined; pyramidal areas distinct from adjacent spore coat. Apex may be somewhat elongate. On smaller abortive forms haptotypic features are commonly masked by development of a thick rugose, more or less triangular cushion which effectively seals the spore apex. Arcuate ridges are inconspicuous but sometimes their termini are weakly defined adjoining the corners of the cushion. Larger abortive forms commonly show haptotypic features more like fertile spores but somewhat less developed and more irregular in character.

Spore coat. — Variable in thickness, generally relatively thick on abortive and considerably thinner, especially in the median areas, on fertile spores. Pyramidal areas of fertile forms are thinner but the more proximal portion immediately distal to the arcuate ridges is thick; the median portion of the spore is membranous and the extreme distal portion may again be somewhat thicker. The most characteristic feature of this genus is the fibrous character of the spore coat in the membranous middle region; thicker parts of the coat also consist of thicker matting of the interlocking, variable width, anastomosing fibrils. A thinner nonfibrous endosporal membrane may be present. The fibrous spore coat is evidently equivalent to the exospore.

Affinities. — *Cystosporites* is a member of the Lepidocarpaceae. It is intimately related to the genera *Lepidocarpon*, *Illiocarpon*, and probably others of this family in which the correlation has not been as definitely established (Schopf, 1941). Spores of *Cystosporites*, although highly specialized with reference to semi-

nal adaptation, appear to be generalized so far as specific differences are concerned. The ornamental patterns which serve to distinguish spores of free-sporing lycopids have evidently undergone extensive reduction if such characteristics were ever present in the line of lepidocarp ancestry. The genus *Cystosporites* thus expresses a broader relationship than that exemplified by other genera in the Lepidocarpaceae, and, so far as is known, is inclusively correlative with the lepidocarp family. Future discoveries may make it possible to restrict this group and establish relationships in greater detail. The spores found within the seeds of lepidocarp species are receiving more detailed study now (Reed, 1941; Darrah, 1941; Hoskins and Cross, 1941; Schopf, 1941) and further studies may show other features of the spore coat that have unsuspected systematic significance.

Zerndt (1930, et seq.) has classified some forms now placed in *Cystosporites*, under *Triletes*. The distinction between free-sporing and seed-bearing lycopids seems at least familial in its importance (Schopf, 1941) and this distinction is most in evidence when the megaspores are compared.

Remarks. — The fertile and abortive megaspores of species of *Cystosporites* are very heteromorphous. In several instances they have been recovered in tetrad groupings from maceration residues of coal. They nevertheless are generally separated from one another so that a system of treatment for the isolated tetrad members both fertile and abortive seems essential for scientific reporting. The characters of the fertile spores are used to identify species, and fertile specimens serve as holotypes for the two species listed below. Isolated abortive spores may be distinguished in classification as formae. The procedure may serve as a practical means of expressing relationships between these heteromorphous spore types and still retain for each of them a nominal distinction. There appear to be no inherent disadvantages in such a policy, as it affords a means of more accurate recording of actual material encountered; only the accrual of additional information can show whether such a practice, in fact, is necessary. If the formae later appear superfluous in some instances and worthy of

actual specific status in others, these changes can be effected without undue taxonomic difficulty or confusion since type material is indicated in all instances.

Cystosporites has an extensive range in the Carboniferous as is best shown by tables of spore distribution given by Zerndt (1937), and so far as is now known is restricted to this period. The type species was described from Illinois No. 6 (Herrin) coal.

1. CYSTOSPORITES BRERETONENSIS Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, pp. 40-42, pl. 3, fig. 5, pl. 8, figs. 1-4.

Triletes cf. *T. giganteus* Zerndt, Schopf, 1936, Illinois Acad. Sci. Trans. vol. 28, no. 2, p. 107, fig. 5 (holotype of *C. breretonensis*).

Triletes cf. *T. giganteus* Zerndt, Schopf, 1936, idem. p. 175.

CYSTOSPORITES BRERETONENSIS forma ABORTIVUS Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, p. 40, pl. 1, fig. 10, pl. 8, fig. 4.

CYSTOSPORITES BRERETONENSIS forma RETICULATUS Schopf, 1938, idem, p. 40, pl. 1, fig. 11.

2. CYSTOSPORITES GIGANTEUS (Zerndt) Schopf, 1938, idem, p. 39.

Triletes giganteus Zerndt, 1930, Acad. polonaise sci. Bull. internat., ser. B, p. 71, pls. 9, 10, and 11.

Type 1 Zerndt, 1931, Acad. polonaise sci. Bull. internat., ser. A, p. 170.

Sporites giganteus (Zerndt) Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 172, pl. 8, fig. 9.

Triletes giganteus Zerndt, 1937, Acad. polonaise sci. Trav. Geol. no. 3, p. 4.

CYSTOSPORITES GIGANTEUS forma VARIUS (Wicher) S. W. and B., comb. nov.

Triletes (Lagenicula) glabratus Zerndt, 1930, Acad. polonaise sci. Bull. internat., ser. B, p. 54, pl. 8, figs. 38-41.

(?) Type 29 Zerndt, 1931, idem, ser. A., p. 175.

Type 30 Zerndt, 1931, idem, ser. A., p. 175, pl. 8, figs. 26-27.

Type 30 Zerndt, 1932, Jahrb. fur das Berg-u. Hüttenwesen in Sachsen. Jahrg. 1932, p. 13A, pl. 1, figs. 1, 2, 3.

Sporites varius Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 4, p. 89, pl. 6, figs. 2, 3, 4, 6.

Genus PARASPORITES Schopf, 1938

Plate 2, figures 16-16b

Symmetry.—Prepollen grains appearing bilateral due to opposing bladders. The fundamental symmetry, clearly shown by the body, is radial.

Shape.—Body nearly spherical, bladders of moderate inflation placed laterally and opposite one another on the spore give an oval external outline. On compression few folds are formed and these generally do not modify the profile unless the plane of the bladders fail to coincide with the plane of compression.

Size.—Relatively large; species attain as much as 300 microns length from one bladder tip to the other.

Ornamentation.—Body wall may be rugose, bladder membrane lightly sculptured.

Haptotypic features.—Relatively inconspicuous and evidently modified in post-tetrad development. Trilete rays often developed with two long rays and one characteristically shorter. One pyramidal area may sometimes be distinguished; except in this area no arcuate marking is evident.

Spore coat.—Body wall (exospore) tending to be dense and of moderate relative thickness; bladder membrane (perispore), relatively thin and quite translucent.

Affinity.—There is considerable probability that the plants represented by *Parasporites* are gymnospermous. The perisporal bladder development is strongest evidence of this. It is still a question whether the genus should be assigned with the Pteridosperms, Cordaitaleans or the Conifers (cf. Schopf, 1938, pp. 47-8).

The genus has some evident claim to affinity with *Florinites*, S. W. and B., *Pityosporites* Seward, *Alisporites* Daugherty, and to *Endosporites* Wilson and Coe. Perhaps it is closest to *Endosporites*, but as these forms are contemporaneous their relationship cannot easily be regarded as direct.

Remarks.—The genus is monotypic being represented only by the species given below which has been found in upper Carboniferous and lower McLeansboro age coals of Illinois. The point upon which greatest emphasis should be placed is that the development of proximal sutures is such as to indicate proximal gametophytic exit similar to *Endosporites* and *Monoletes*. Aside from this and its rather large size *Parasporites* has pollen

grain characteristics. It may represent a veritable "prepollen".

1. PARASPORITES MACCABEI Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, pp. 48-9, pl. 1, fig. 6, pl. 7, figs. 1-3.

Genus CIRRATRIRADITES Wilson and Coe, 1940

Plate 3, figures 21, 21a, 21b

Symmetry.—Spores trilete, radial.

Shape.—Moderately oblate spheroidal, with a strongly projecting equatorial flange. The flange may assume a triangular horizontal outline due to emphasis of the trilete rays, or it may be nearly circular; the spore body is circular or slightly triangular. When compressed, few folds are evident and, because of the flange and oblate shape of the body, the plane of flattening nearly always corresponds with that of the flange.

Size.—Spores of various species range from about 40 to over 100 microns in overall diameter.

Ornamentation.—Commonly showing a pattern having its primary emphasis along radial lines; may consist of ridges more or less anastomosing to the point of becoming a reticulation, or surfaces may be nearly free of ornamental ridges and most of the surface smooth, granulose or finely punctate. Some species show a unique type of distal ornamentation consisting of one or several thinner areas with rather prominent margins. The flange is often more or less radially striated and in addition may develop one or two concentric bands of irregular thickening. The pyramidal areas are not particularly distinguished by ornamentation.

Haptotypic features.—Trilete rays relatively strongly developed and extended to the equator, oftentimes a line of thickening continues to the edge of the flange. Lips are frequently strongly demarcated and raised above the spore body; the suture lines are attenuate but distinct. No arcuate ridges are developed distinct from the flange and, in fact, the flange may be taken to represent a hyper-development of these haptotypic formations. The flange is usually relatively broad, sometimes comprising more than half the total spore diameter. It is definitely distinguished from the spore body, being thinner than the body wall and more translucent; the interradial flange width is often some-

what less than that opposite the rays. The margin of the flange is often minutely to rather coarsely serrate.

Affinity.—Spores of *Cirratriradites* are not yet definitely correlated with any major plant group. Their most likely affinity seems to be with the lycopods but known types of *Lepidostrobus* microspores are usually smaller and generally possess no comparable development of the flange. Certain zonate types of *Triletes* spores bear a superficial resemblance to *Cirratriradites* but so far as is known now there is no inherent correlation between structure of megaspores and microspores where heterospory is as highly developed as it is in *Triletes*. There is in fact no essential evidence to show whether spores of *Cirratriradites* functioned as microspores or isospores. The Carboniferous existence of isosporous lycopods is still most firmly supported only on theoretical grounds but they could possibly be represented by *Cirratriradites*.

Some authors have confused *Cirratriradites* spores with those of genera (*Endosporites*, *Spencerites*, etc.) which possess perisporal bladder development in the equatorial plane. Such resemblance as there is, is certainly only superficial.

Raistrick's A₇, A₈, and C₅ (cf. Raistrick 1935, 1937, 1938) belong here; likewise, possibly D₂ in part. As given by Knox, (1938, 1942) D₁₂ is definitely referable to *Cirratriradites*. Types 1 and 9 of Millott (1939) without much question belong in this genus. The spores illustrated by Reinsch (1884, p. 22) in plate 15, figs. 1a and 1b as types 222 and 223 from Zwickau, Saxony, are characteristic of it.

Remarks. — Thirteen previously described species are included in the list below, all but one of which, *C. maculatus* the genotype, represent new name combinations.

Spores of this character are frequently encountered in American coals and additional species will subsequently be described. The group shows such general agreement in numerous characteristics that a considerable degree of natural relationship is attributed to it.

1. CIRRATRIRADITES ARGUTUS (Ibrahim) S. W. and B., comb. nov.

Zonales-sporites argutus Ibrahim, 1933, Sporenformen des Aegirhorizonts, pp. 31-32, pl. 6, fig. 55.

2. CIRRATRIRADITES (?) CICATRICOSUS (Ibrahim) S. W. and B., comb. nov.

Sporonites cicatricosus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 447, pl. 14, fig. 2.

Zonales-sporites cicatricosus (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 31, pl. 1, fig. 2.

3. CIRRATRIRADITES FAUNUS (Ibrahim) S. W. and B., comb. nov.

Sporonites faunus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 447, pl. 14, fig. 4.

Zonales-sporites faunus (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 28, pl. 1, fig. 4.

4. CIRRATRIADITES FORMOSUS (Ibrahim) S. W. and B., comb. nov.

Sporonites formosus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 447, pl. 14, fig. 10.

Zonales-sporites saturni (Ibrahim) Ibrahim, in part, 1933, Sporenformen des Aegirhorizonts, p. 30, pl. 1, fig. 10.

5. CIRRATRIRADITES (?) GRACILIS (Zerndt) S. W. and B., comb. nov.

Triletes gracilis Zerndt, 1937, Acad. polonaise sci. Bull. internat., ser. A., p. 586, pl. 12, figs. 1-10.

Type 46 Zerndt, 1937 (idem).

Note.—Species exceptionally large (300 μ), otherwise in close generic agreement.

6. CIRRATRIRADITES MACULATUS Wilson and Coe, 1940, Am. Midland Naturalist, vol. 23, no. 1, p. 183, fig. 7.

Note.—Reexamination of the type material suggests the trilete apex is ordinarily normally developed and that the apical opening originally described is not of general occurrence. Sculpturing simulating it may occur distally.

7. CIRRATRIRADITES (?) PEACOCKI (Berry) S. W. and B., comb. nov.

Zonales-sporites peacocki Berry, 1937, idem, vol. 18, p. 156, fig. 5.

8. CIRRATRIRADITES PENNINGTONENSIS (Berry) S. W. and B., comb. nov.

Zonales-sporites penningtonensis Berry, 1937, idem, p. 156, fig. 3.

9. CIRRATRIRADITES RARUS (Ibrahim) S. W. and B., comb. nov.

Zonales-sporites rarus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 29, pl. 6, fig. 53.

10. CIRRATRIRADITES SATURNI (Ibrahim) S. W. and B., Comb. nov.

Sporonites saturni Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 448, pl. 15, fig. 14.

Zonales-sporites saturni (Ibrahim) Ibrahim, in part, 1933, Sporenformen des Aegirhorizonts, p. 30, pl. 2, fig. 14 (non pl. 1, fig. 10).

Zonales-sporites saturni (Ibrahim) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 149; pl. 7, fig. 23.

Note.—Ibrahim (1933) came to the conclusion that *Sporonites formosus* Ibrahim (1932) was conspecific with *C. saturni*. Very little information is provided to support this and, since the figures appear to show specific differences, it appears desirable to keep them separate for a time at least.

11. CIRRATRIRADITES TENUIS (Loose) S. W. and B., comb. nov.

Sporonites tenuis Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 450, pl. 18, fig. 34.

Zonales-sporites tenuis (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 149.

12. CIRRATRIRADITES VENUSTUS (Loose) S. W. and B., comb. nov.

Sporonites venustus Loose, 1932 Neues Jahrb., Beilage-Band 67, Abt. B., p. 450, pl. 18, fig. 36.

Zonales-sporites venustus (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 149.

13. CIRRATRIRADITES ZONALIS (Loose) S. W. and B., comb. nov.

Zonales-sporites zonalis Loose, 1934, idem, vol. 4, no. 3, p. 148, pl. 7, fig. 5.

Genus ENDOSPORITES Wilson and Coe, 1940

Plate 2, figures 14-14b

Symmetry.—Spores trilete, radial.

Shape.—Moderately flattened elliptical in transverse plane, in axial plane round to oval or elliptical or slightly triangular; body wall more spherical than the bladder. When compressed the spores most commonly show good proximo-distal orientation. The spore body is not generally folded but the bladder membrane more commonly shows irregular plication. The bladder profile at the margin of the spore corresponds to the profile of folds, being straight or evenly rounded, and thus easily distinguishable from simple flanges of zonate forms that superficially resemble *Endosporites*.

Size.—Ranging in various species from about 50 to possibly 300 microns total diameter. The spore body generally is less than one-half of the full diameter.

Ornamentation.—Surfaces of bladder are levigate to granular or punctate; a fine meshed reticulation pattern is commonly present but this is probably on the *inside*, rather than on the external bladder

surface. The spore body is less definitely ornamented although the bladder pattern may appear superimposed on it. Emphytic ornament seems to be the same for proximal and distal surfaces.

Haptotypic features.—Trilete rays commonly extend to the periphery of the spore body and thickened continuations from them may carry on to the bladder membrane. The lips are oftentimes upraised and definite, the suture line distinct. Sometimes a thickening is present on the bladder membrane which corresponds to arcuate ridges.

Spore coat.—The bladder (perisporal) membrane is quite thin and translucent; its reticulation tends to add somewhat to the thickness as seen in marginal profile. The body wall is substantially thicker although also quite translucent, and corresponds to the exosporal layer. In a few instances thin membranous, almost hyaline, endosporal membranes have been observed within the exospore and shrunk from it. The suture lines are not distinct on these, but three clear-cut endosporal apical papillae occur at the juncture of pyramic apices.

Affinities.—*Endosporites* is related to some of the Pennsylvanian Cordaitaleans. They correspond to spores observed by Wilson in male strobili, and Schopf has found well preserved specimens in such abundant association with Cordaitean leaves, other plant fossils being infrequent, that no other conclusion seems permissible. It should be emphasized, however, that the pollen grains Florin (1936) described in *Cordaianthus* fructifications obtained from the French Stephanian are evidently generically distinct and of more advanced structure.

Raistrick's types C₁ and C₄ without much question belong to *Endosporites* (Raistrick and Simpson, 1933; Knox, 1938). Type 629 of Reinsch (1884, p. 61, pl. 48, fig. 252A) from the Blatterkohle and Stigmarienkohle of Metschowk (in central Russia) and probably others less easy to interpret from his drawings, also belongs to *Endosporites*.

Remarks.—The distended bladder membrane is the most characteristic feature of certain gymnospermous pollen grains. The expansion of the bladder is various in the several groups which are known as

Parasporites, *Cordaianthus*, *Alisporites*, *Caytonanthus*, *Pityosporites* and *Endosporites*, as well as in modern podocarps and Abietineae. There is good reason to believe that bladders of this type are homologous structures, which may have undergone progressive and regressive development at various times within the broad confines of this alliance, but nevertheless largely preserve their identity throughout.

Endosporites shows such evident development of proximal haptotypic structures that gametophytic exit was quite evidently from the proximal pole as in the cryptogams. Florin, working with excellently preserved silicified material, has shown that in some late Pennsylvanian (Stephanian) forms the haptotypic features were vestigial and in mature forms present only as a surface imprint on the bladder membrane which does not even maintain contact with the spore body. The bladder and body are in contact distally, however, and prothallial cells line the body cavity except at this point. Thus in these advanced forms germinal exit must have been distal as it is in pollen of all modern conifers. Pollen-like types of this sort having indication of proximal exit have been termed "prepollen," following Renault, and its significance has been discussed elsewhere (Schopf, 1938; pp. 14 and 15, 48). *Endosporites* male spores are evidently prepollen in this sense.

Eight previously described species are listed below, only one of which is queried. The genus is widely distributed both in America and in Europe. The genotype species, *E. ornatus* Wilson and Coe, is from Iowa coal of Des Moines age.

1. *ENDOSPORITES ANGULATUS* Wilson and Coe, 1940, Am. Midland Naturalist, vol. 23, no. 1, p. 184, fig. 1.
2. *ENDOSPORITES GLOBIFORMIS* (Ibrahim) S. W. and B., comb. nov.
Sporites globiformis Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 447, pl. 14, fig. 5.
Zonales-sporites globiformis (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 28, pl. 1, fig. 5.
Zonales-sporites globiformis (Ibrahim) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 148.
3. *ENDOSPORITES (?) KARCZEWSKII* (Zerndt) S. W. and B., comb. nov.

Triletes karczewskii Zerndt, 1934,
Acad. polonaise sci. Trav. Geol. no. 1, p.
27, pl. 31, fig. 3.

Note.—Agrees well with *Endosporites* though
larger than most species.

4. *ENDOSPORITES ORNATUS* Wilson and Coe,
1940, Am. Midland Naturalist, vol. 23, no.
1, p. 184, fig. 2.

Spore 6, Wilson and Brokaw, 1937,
Iowa Acad. Sci., vol. 44, pp. 129-130, fig. 6.

5. *ENDOSPORITES PELLUCIDUS* Wilson and Coe,
1940, Am. Midland Naturalist, vol. 23, no. 1,
p. 184, fig. 3.

Spore 1, Wilson and Brokaw, 1937,
Iowa Acad. Sci., vol. 44, pp. 128-129, fig. 1.

6. *ENDOSPORITES ROTUNDUS* (Ibrahim) S. W.
and B., comb. nov.

Zonales-sporites rotundus Ibrahim,
1933, Sporenformen des Aegirhorizonts, p.
31, pl. 8, fig. 73.

7. *ENDOSPORITES RUGATUS* (Ibrahim) S. W.
and B., comb. nov.

Zonales-sporites rugatus Ibrahim, 1933,
idem, p. 31, pl. 8, fig. 70.

8. *ENDOSPORITES VOLANS* (Loose) S. W. and
B., comb. nov.

Sporonites volans Loose, 1932, Neues
Jahrb., Beilage-Band 67, Abt. B, p. 451,
pl. 18, fig. 46.

Reticulatisporites volans (Loose) Ib-
rahim, 1933, Sporenformen des Aegirhor-
izonts, p. 36.

Zonales-sporites volans (Loose) Loose,
1934, Inst. Paläobot. Arb., vol. 4, no. 3,
p. 149.

Note.—Trilete rays are shorter than is com-
mon in this genus.

Genus TRIQUITRITES Wilson and Coe, 1940

Plate 3, figures 20-20b

Symmetry.—Spores trilete; radial.

Form.—Oval to elliptical in vertical
plane, distal side sometimes slightly more
inflated than the proximal; in the equato-
rial plane triangular in outline, corners
rounded or truncate subangular and some-
times extended, sides slightly convex to
strongly concave in profile. Folds are
seldom induced by compression due to
good preferential orientation coinciding
with the horizontal plane of the spores;
forms more inflate distally are indicated
through a tendency of the corners to be
directed slightly upwards exaggerating the
natural thickening of the spore coat on the
angles.

Size.—Spores of various species com-
monly range from 35 to 70 microns in
mean diameter.

Ornamentation.—Surfaces levigate to
granulose and mildly verrucose, angular
areas sometimes more highly ornamented.
Emphytic ornamentation of proximal and
distal surfaces is about the same.

Haptotypic structures.—Trilete rays ex-
tended nearly to the margin of the body
cavity; lips sometimes rather thick and
prominent, but usually not particularly
demarcated. Arcuate ridges lacking; like-
wise, no flange in the usual sense is de-
veloped though extreme extensions of the
spore coat at the angles may simulate a
partial flange.

Spore coat.—Characterized by gross in-
equalities in exospore thickness; spore
coat is thickest on the angles opposite ends
of the rays and thinnest in the central
distal and possibly to a somewhat lesser
extent on the interradial areas. Actual
thickness of different parts of the wall
in various species varies greatly although
the relations of thicker and thinner areas
of the spore coat is rather constant.

Affinity.—*Triquitrites* cannot be as-
signed to any major plant group at the
present time although the character of the
spore coat seems so individualistic that
the genus is considered to correspond with
natural plant relationship. The features, in
general, seem to agree best with spores of
filicineans.

Type 10 of Millott (1939) belongs to
Triquitrites and probably type D₁₀ of Rai-
strick (1938). Type D₇ (Raistrick, 1934,
1935, 1938) shows more extreme thicken-
ing of the radial angles of the spore coat
so that it is evidently closely related to
this genus, though it is a question whether
it should be classified as *Triquitrites* or
distinguished from it. Knox' Type 4K
(1942) is clearly congeneric. Spores of
the same sort but even more extreme have
been illustrated by Reinsch (1884) in his
plate 3, figures 34-42, corresponding to
his type diagnoses, nos. 345, 347, 349, 353,
354, 362, 363, 365, 373. Reinsch also
illustrated other forms which are doubt-
less congeneric with *Triquitrites* in his
types 58, 200, 341, 342, 348, 355, etc.
Type 58 shown on his plate 15, figure
18A, from Zwickau, Saxony, is remi-
niscent of some, possibly overmacerated,
specimens of the genotype species.

Remarks.—Five named species are as-
signed to *Triquitrites*; three represent new
name combinations. Other species are

known from American coals and will subsequently be described. The numerous spores illustrated by Reinsch (1884) in the *Micro-Paleophytologia* show best the variation in structure encountered in this group. The spores with highly exaggerated angular thickenings were mostly derived from localities in Russia where the coals probably are of Lower Carboniferous age. D_{10} and D_7 types of Raistrick (1938) were chiefly obtained from the Lower Carboniferous of England. Pennsylvanian age species are much more moderate in spore coat thickness and the interradial and distal membranes are frequently less than 3 microns thick, as in the four species which have been described and named. The angles are more than twice as thick, however, and their relationship thus seems definitely indicated. Nevertheless, it may be desirable that the thicker walled more ornate and radially extended forms be generically segregated when detailed modern information becomes available for the older species. The tendency toward seeming simplification in spore coat structure of late Carboniferous plants as contrasted with earlier members of the same alliance has also been noted in members of the *Lagenicula* and *Aphanozonataeae* sections of *Triletes*.

1. TRIQUITRITES ARCULATUS Wilson and Coe, 1940, Am. Midland Naturalist, vol. 23, no. 1, p. 185, fig. 8.

Note.—Type material bears a moderate to sparse verrucose flecking (areas of thickening) on proximal and distal surfaces, possibly due to overmaceration.

2. TRIQUITRITES SPINOSUS Kosanke, 1943, Am. Midland Naturalist, vol. 29, no. 1, p. 128, pl. 3, figs. 2, 2a, 2b.
3. TRIQUITRITES TRIBULLATUS (Ibrahim) S. W. and B., comb. nov.

Sporonites tribullatus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 448, pl. 15, fig. 13.

Laevigatisporites tribullatus (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, pp. 20-21, pl. 2, fig. 13.

Valvisi-sporites tribullatus (Ibrahim) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 152, pl. 7, fig. 21.

4. TRIQUITRITES TRIGONAPPENDIX (Loose) S. W. and B., comb. nov.
5. *Valvisi-sporites trigonappendix* Loose, 1934, idem, p. 152, pl. 7, fig. 17.
6. TRIQUITRITES TRITURGIDUS (Loose) S. W. and B., comb. nov.

Sporonites triturgidus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 449, pl. 18, fig. 32.

Valvisi-sporites triturgidus (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 151.

Genus EQUISETOSPORITES Daugherty, 1941

This genus recently described from Triassic age beds in southwestern United States is mentioned here because of its important bearing on recognition of fossil spores of certain Equisetalean plants. The genus is monotypic, including only *E. chinleana* as given below, whose noteworthy feature is the presence of elaters very similar to those characterizing the modern genus. The validity of the name *Equisetosporites* rests on the belief that these forms should be distinguished from spores of *Equisetum*. It appears there is adequate support for this view since Daugherty, in a personal communication, states "in all cases *Equisetum*-like plants of the Triassic have proven to be quite different when the record is complete enough to allow specific determination." Thus until further evidence is available, it would seem unwise to emphasize the modern aspect of this fossil form. Its discovery nevertheless adds an important item of information to the record.

Knox examined spores of fifteen species of *Equisetum* and reports (1938, pp. 439-40) them to be invariably spherical, 30 microns to 35 microns in diameter, and always thin walled. In all these species the spore wall was faintly granular. Elaters of somewhat varied character are present on all modern species of *Equisetum*. In commenting on Raistrick's B₃ type, which she recognizes is very probably of calamarian affinity, Knox remarks (pp. 461-3) on

the same globose form with thin wall and absence of ornamentation . . . the unusual development of elaters and no trace of the triradiate mark.

She cites Halle's description of Rhaetic and Triassic-age *Equisetum* spores (Halle, 1908) in which the trilete commissure is clearly seen but which show no trace of elaters. Halle assumed that even if elaters had been present they would have been removed by maceration procedure. Needless to say, this aspect

must always be considered. Nevertheless, the spores recovered by Halle were typical of calamarians (cf. Hartung, 1933) and isolated spores of this character must be classed with *Calamospora* n. gen. as described below. *Equisetosporites chinleana* is quite different and marks the advent of a more distinctly modern character in this ancient and persistent order of plants. Evidently a reduction in importance of haptotypic features has occurred and concurrently the perisporal adaptation represented by elaters has come into existence. Careful study of the fossil spores may be expected to indicate more completely the relationship and distribution of equisetalean types.

The type of the single species of *Equisetosporites* now known has been made available to us for examination through the kindness of Prof. Ralph W. Chaney and the following description, which is somewhat more detailed than Daugherty's, is offered for comparison with the other descriptions given in this paper. This specimen (No. 1562 of the California Museum of Paleontology) is adequately illustrated by Daugherty in the figure cited below.

Symmetry.—No trace of original tetrad configuration visible.

Shape.—Body spherical (type specimen elliptical, 30 x 37½ microns, due to one elongate taper-point fold).

Ornamentation.—Body wall essentially smooth showing very slight surface undulation.

Spore coat.—Thin, apparently slightly less than a micron in thickness. In spite of this the body is deep brown color as viewed by transmitted light.

Elaters.—Probably four in number, having their attachment close together; each one possibly about 70 microns long, band-like, about 4 microns wide, with slight irregularities; yellowish translucent. Elater ends truncated, tapering for a short distance, not at all broadly terminated. (Two of the four free ends are shown at the right edge and overlapping the spore body in Daugherty's fig. 4.) Evidently the elaters tended to spirally encircle the spore body but they have been displaced on the specimen at hand.

1. *EQUISETOSPORITES CHINLEANA* Daugherty, 1941, Carnegie Inst. Washington Pub. 526, p. 63, pl. 34, fig. 4. Age, Triassic.

Genus *ALISPORITES* Daugherty, 1941

Plate 2, figure 12

This genus, like the preceding, is monotypic, the sole species yet described being of Triassic age from Southwestern United States. It is included in this paper because spores of Permian age which are probably referable to it have been found, and because there seems some basis for relating it to *Parasporites* and *Pityosporites*. The only description is that of the genotype species, *A. opii*, given below (Daugherty 1941, p. 98).

"The spores are large, averaging 100 to 110 microns in length and having two large membranaceous wings with reticulate markings. They are spherical to ovate in dorsal view,¹¹ having a rather thick exine and a single fusiform furrow."

Pollen grains of Caytoniales, when isolated, without much doubt should be classified under *Alisporites* unless there is particularly good evidence for referring them to *Caytonanthus*. Harris (1941) has distinguished *Caytonanthus kochi*, *C. oncoides*, and *C. arberi* largely on the basis of differences in their pollen and has suggested their correlation with species of *Caytonia* and *Sagenopteris* found in the same deposits. All evidence seems to point to the validity of Harris' conclusions, yet further information will probably tend to modify the picture. For example, certain of the spores isolated from the Stassfurt salt deposits by Lück (1913) seem properly referable to *Alisporites* and similar to spores of *Caytonanthus*, but probably few would suggest that the genus *Caytonanthus* should be identified on that slender basis. The fructifications which bore the Permian *Alisporites* would be presumed to differ generically due to the general tendency of such organs to be evolutionarily plastic and amenable to structural modification. The generic features of pollen grains seem in general to be more conservative. But whether organs are evolutionarily conservative or amenable to biocharacter al-

¹¹ The terms dorsal and ventral tend to be ambiguous in description of pollen grains, particularly unless some further explanation is given. Probably "dorsal" as used here refers to the proximal side, i.e., the side which was internal and adjoined the other members of the original tetrad.

teration, the important point relates to recognition of the degree of change that is manifested and of the fact that bi-character modification has proceeded at different rates in the different organs and parts of the plant life cycle. In order that fossil identifications may be scientifically trustworthy these principles should be more widely acknowledged. *Alisporites* is a designation that should be very useful in reporting the occurrence of caytonian spores and others of the same sort which perhaps may not even be necessarily referable to that group. Whether the Caytoniales are worthy of ordinal distinction is perhaps subject to some question now that Harris (1941, 1940) has shown so convincingly that they are gymnospermous and have no particular connection with angiosperms. Likewise whether they should be termed pteridosperms is still perhaps too much a matter of individual opinion. The problem of caytonian relationship with other gymnospermae is a perplexing one which may find its truest solution in the exacting study of fossil pollen grains similar to *Alisporites*, *Parasporites*, and *Pityosporites*.

The more adequate generic definition of *Alisporites* should be taken up in connection with such studies. Daugherty's generic distinction of these interesting plant microfossils is a forward step which will provide a much more precise means of referring to them. They can be distinguished from spores of *Parasporites* by their lack of a trilete commissure and probably in their distal mode of exit; from *Pityosporites* in having the bladders placed opposite one another and not inclined distally, also in their lack of a thick proximal cap. Although it would seem possible to recognize morphologic homologies between the parts of *Alisporites* pollen and the spores of *Endosporites* and those of other cordaitaleans, these genera seem more distantly related and are easily distinguished. Pollen similar to that of *Lebachia* and *Walchianthus*, now placed in the new genus *Florinites* (p. 56), is distinguished from pollen of *Alisporites* by the presence of an annulate bladder.

1. ALISPORITES OPII Daugherty, 1941, Carnegie Inst. Washington Pub. 526, p. 98, pl. 34, fig. 2.

2. ALISPORITES spp. ?

Pollen Forms I, II, and III, Lück, 1913, Beitrag zur Kenntnis des älteren Salzgebirges im Berlepsch-Bergwerk bei Stassfurt nebst Bemerkungen über die pollenführung des Salztones, pp. 29-31, figs. 53-56, 58-59.

Genus CALAMOSPORA S. W. and B., gen. nov.

Plate 3, figures 22-22b; text figure 1

Symmetry.—Spores trilete; radial.

Shape.—Spherical or nearly so; when compressed, readjustment to a disk-like form leads to formation of characteristic sharp taper-point folds of variously crescentic or narrowly lenticular outline. Sometimes the spores are folded double so that the whole external outline is sharply lenticular. Such folds are one of the characteristic features of the genus.

Size.—Highly variable from about 40 microns (or smaller in some abortive specimens), to several hundred microns in diameter.

Ornamentation.—Spores are characteristically very smooth in general appearance; on closer inspection they may be minutely granulose or slightly rugose. There may be very slight differentiation of proximal pyramidal areas shown by this almost negligible emphatic marking. Larger spores often possess a high gloss when observed by reflected light.

Haptotypic structures.—Trilete rays notably short; usually they do not exceed one-half the length of the spore radius. The suture line is distinct and attenuate; sometimes moderate lips are developed. Arcuate ridges are commonly not distinguishable although they may be present as slight rounded thickenings. In some forms the pyramidal areas have a somewhat different surface texture than the rest of the spore coat.

Spore coat.—Relatively thin. Spores less than 100 microns diameter are generally yellowish and highly translucent; larger spores (which certainly are mostly megaspores) are progressively less translucent as the wall thickness increases relative to the spore diameter. Actual wall thickness thus is highly variable in various species, ranging from about 15 microns in forms over half a millimeter in diameter, to less than 2 microns in those smaller than 100 microns. A very thin

endosporal membrane may be present, oftentimes shrunken away from the exosporal coat.

Affinity.—Hartung's (1933) investigation of spores in fructifications that were referred to six different genera allied with the calamarians has provided an excellent basis for systematic treatment of plants of this sort which are only represented by their isolated spores. In general, the spores do not appear to lend themselves to grouping into restricted generic alliances but show a rather generalized character. Certain species may easily be distinguished by spore differences but generic characteristics (in terms of the fructifications) are not present or at least not yet recognized. The genus *Calamospora* therefore must be regarded as coordinate with a large proportion of the calamarians as they are now reported. In addition, Nemejc has shown that spores isolated from *Noeggerathiosporbus* (Nemejc, 1935) and from *Discinites* (*ibid.*, 1937) are similar in character and he regards this as sound evidence of alliance between these and the articulate groups although the degree of relationship is still difficult to evaluate.

For the present *Calamospora* is regarded as allied to the groups just mentioned and probably is also correlative with some Mesozoic equisetaleans (cf. remarks on *Equisetosporites*, p. 47). Thus it is one of the most broadly related of the groups regarded as showing evidence of actual natural relationship. There is no question but that it would be advantageous to subdivide the group into sections or into several genera but such a treatment does not seem practicable now.

Zerndt (1934) has obtained spores of generally similar character by maceration of coal and refers those over 200 microns in diameter to his Type 2. Several distinct species of *Calamospora* are represented by it. He regards these forms as pertaining to the Calamite group; however, there appears to be no very definite evidence of their generic correlation. Their character nevertheless is indicative of affinity with the calamarian branch of the Articulateae. Many of the type B₃ spores of Raistrick (1933, 1934, etc.) are

referable to this genus but probably not all of them should be classed here. There are a few forms of *Punctati-sporites* that are very similar in definable features but nevertheless show differences of habit that set them apart from *Calamospora*. Some of the B₃ types Raistrick has illustrated have trilete rays more extended than they generally are in spores of *Calamospora*, and it is possible that some calamosporean forms may have been included in his type B₅. Miss Knox (1938, p. 461) has remarked on the affinity the B₃ spores and compared them with spores of *Calamostachys binneana* and *Cheirostrobos pettycurensis*.

Remarks.—*Calamospora* is unique among genera typically represented by plant spores in that megaspores, microspores, and probably isospores, are included in it. The Calamarians seem not to have developed as specialized a type of heterospory as quickly as the lycopods or other groups, and it has been generally doubted that they ever achieved a comparable state of heteroporous development. Elias believes, however, that seed-like bodies were developed in the group of *Annularia stellata* and he has distinguished these forms as *Carpanularia* (Elias, 1931). This material was obtained from beds of lower Des Moines age. Such a view also was expressed by Renault and others of the French school when calamites with secondary wood were regarded as gymnosperms, but at least a very large part of the seed evidence then was based on chance association with seeds that we now know have no calamite relationship. No seed megaspores have yet been reported in the bulbous bodies of *Carpanularia* and this or some similar type of evidence will probably be necessary before their seed-like nature can be regarded as established.

One feature stands out in the sporogenous sequence of the calamite alliance. More evidences of incipient heterospory are observable there than in any other fossil group. Apparently normal spores of two sizes but otherwise similar in appearance are found in adjacent sporangia. The larger spores frequently are admixed with abortive forms in various stages of development. Sporangial masses com-

posed of abortive and fertile spores have also been observed in coal maceration residues (Schopf, 1938, p. 51). Most noteworthy is the fact that large spores exceeding half a millimeter in diameter show characters very similar to those of less than 100 microns in diameter. Although heterospory was well established, a seemingly continuous size gradation exists between the largest members and the smallest with little but relative size as a distinguishing feature. Spores in fructifications which are less than about 90 microns in diameter frequently are regarded as microspores and those that exceed that size often appear to represent megaspores. But in different species and in general there seems to be no exact way to distinguish between them unless the contrasting size spore is present in the same fructification for comparison.

Species distinguished within *Calamospora* probably include spores of one morphologic category only and thus heterosporous plants may oftentimes be recorded under two specific names. This is no serious disadvantage if we are interested in obtaining the most precise information that such material can provide. If records thus integrated are obtained, it will eventually be possible to trace the correlation of large and small spore forms in some instances. It is doubtful that the majority will soon be resolvable in this fashion, however, and in the meantime there is need for the most accurate reporting of this material that is feasible.

Six species previously described and named are listed below, one of which is queried, and one new species described. Spores of this generic character are common in many American coals and this genus will be useful in providing a systematic means of recording them. It has seemed advisable to describe *C. hartungiana*, one of the characteristic American forms, to serve as a genotype of *Calamospora* rather than utilizing the published description of a species previously established. Most of the descriptions already published are less detailed than desired and are still insufficiently illustrated for purposes of close comparison.

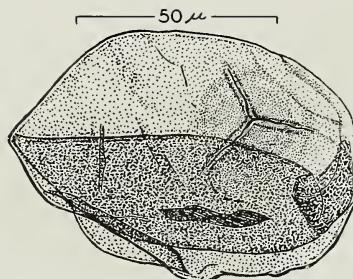


FIG. 1—*Calamospora hartungiana* sp. nov., drawing from microprojection of holotype.

1. CALAMOSPORA HARTUNGIANA Schopf, sp. nov.

Text figure 1.

Description.—Spores spherical, compressed to polygonal or acutely lenticular outline, generally with several more or less lunate lenticular folds. Total spore diameter ranges from 80-100 microns where the outline is not foreshortened by obvious folds. Trilete rays about one-fourth of spore diameter, sutures distinct and slightly undulating, lips low but definite of from less than one to two microns width on either side of the suture. Arcuate ridges may be regarded as lacking but the pyramidal areas are slightly thicker and darker by transmitted light than the rest of the spore coat and have slightly coarser surface texture (*kontakthof*). Spore coat thin, one micron or less, generally yellowish translucent or somewhat red when light is transmitted through numerous thicknesses due to folds or the overlapping of several spores. Spore coat minutely rugose to granular; at low magnification the surface appears quite smooth.

Calamospora hartungiana corresponds in general with spores Hartung (1933) obtained from fructifications of *Macrostachya* and *Paleostachya*, some species of which are described as having a similar "kontakthof." He suggests that microspores and isospores of the Calamarians range from 60-150 microns in diameter, and spores of the species just described presumably would fit one of those categories. Probably much more needs to be known of the spores of calamarian fructifications in order to be certain of this, but there can be no doubt as to the general affinity of *C. hartungiana*.

The specimens occur fairly abundantly in the 8- to 10-inch coal of the Macoupin cyclothem (middle McLeansboro age) which is exposed along Salt Fork of Vermilion River northwest of Fairmount, Vermilion County, Illinois. Spores of this sort occur in spore masses 2 mm. or more in length, as well as isolated among the other materials in the residue. The holotype specimen illustrated (text fig. 1) was separated from a spore mass of this sort when the material was being mounted in diaphane. Thus numerous other specimens have also been available for comparison. The size of the spore masses and number of spores loosely pressed together in them (several hundred, although the masses

obviously are only incomplete contents of single sporangia) gives a little additional information on the *Calamospora* fructification.

The holotype is from slide Y of maceration 90, deposited in the Illinois Geological Survey collections, Urbana.

2. *CALAMOSPORA LAEVIGATUS* (Ibrahim) S. W. and B., comb. nov.

Laevigati-sporites laevigatus Ibrahim, 1933, Sporenformen des Aegirhorizonts, pp. 17-18, pl. 4, fig. 46.

Laevigati-sporites laevigatus Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 146, pl. 7, fig. 36.

(*Calamiti?*)-*sporites laevigatus* (Ibrahim) Wicher, 1934, idem, vol. 4, no. 4, p. 172.

3. *CALAMOSPORA MICRORUGOSUS* (Ibrahim) S. W. and B., comb. nov.

Sporonites microrugosus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 447, pl. 14, fig. 9.

Laevigati-sporites microrugosus (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, etc., p. 18, pl. 1, fig. 9.

4. *CALAMOSPORA MUTABILIS* (Loose) S. W. and B., comb. nov.

Calamiti?-*sporites mutabilis* Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 451, pl. 19, figs. 50a-c.

Calamiti?-*sporites mutabilis* (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 145.

5. *CALAMOSPORA (?) OBESUS* (Loose) S. W. and B., comb. nov.

Sporonites obesus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 451, pl. 19, fig. 49.

Laevigati-sporites obesus (Loose) Ibrahim, 1933, Sporenformen des Aegirhorizonts, etc., p. 19.

Laevigati-sporites obesus (Loose) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 145.

6. *CALAMOSPORA PALLIDUS* (Loose) S. W. and B., comb. nov.

Sporonites pallidus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 449, pl. 18, fig. 31.

Punctati-sporites pallidus (Loose) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 21.

Punctati-sporites pallidus (Loose) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 146.

7. *CALAMOSPORA PERRUGOSUS* (Loose) S. W. and B., comb. nov.

Laevigati-sporites perrugosus Loose, 1934, idem, p. 145, pl. 7, fig. 13.

Genus *REINSCHOSPORA* S. W. and B., gen. nov.

Plate 2, figures 11-11b; text fig. 2

This genus appears to include the spores Reinsch (1884) designated as his Subdivisio III of his Subtribus I, *Nucleus triangularis*. The genus is therefore appropriately designated in honor of Reinsch. His description (loc. cit. p. 7) of the subdivision is as follows (free translation from Latin):

Exospore thin (1/24-1/40 of the transverse diameter), smooth or ornamented with granules disposed variously in regular series. Body margins armed with a simple series (sometimes duplicate) of dentiform juxtaposed spines, gradually decreasing (in length) from the central margins toward the angles.

This diagnosis has no taxonomic status although it (and others given by Reinsch) may be quite worthy of validation. One naturally hesitates to apply names on the basis of Reinsch's descriptions and figures because of uncertainty as to the sources and present location of the types. Also, modern interpretations may vary considerably from his as to the significance of certain morphologic features. The point which should be emphasized is that much of Reinsch's work is of value in extending our knowledge of spore form variation, particularly when essential confirmation can be obtained from additional material recently prepared. Thus the forms Reinsch described in his subdivision III are structurally clarified by study of American forms of *Reinschospora* and there is little doubt that three or four still unnamed species have been discovered in his studies. However, there is no particular occasion to propose names for these until similar new material is at hand or the source defined for his old types (if they are preserved) and their character confirmed. The following new generic diagnosis has been constructed on the basis of newer work but it also takes cognizance of the structural features unmistakably shown by Reinsch.

Symmetry.—Spores radial, trilete.

Shape.—Body lenticular to flattened elliptical in the axial plane; subtriangular in transverse plane, corners rounded, sides slightly convex or concave in outline. A fimbriate flange, broadest in the interradial region and very narrow or absent on the corners, may be present to modify

the marginal outline. In some forms the interradial appendages may be dissected into a row of spines, their ends similar to the flange in marginal contour. When compressed, folds are relatively infrequent due to preferred sedimentary orientation parallel to the transverse plane of the spores.

Size.—Forms now known range from about 30 to 85 microns in diameter.

Ornamentation.—Body smooth to granulose; flange is closely striate to markedly fimbriate, sometimes so incised as to form a row of apiculae, long in the interradial region and much shorter toward the corners.

Haptotypic structures.—Trilete rays well defined and extended nearly to the corners of the spore body; it is uncertain whether the fimbriate flange can be interpreted as equivalent to an arcuate ridge since, contrary to usual arcuate ridge development, it is least evident opposite the ends of the rays. Reinsch has illustrated forms with granules in rows paralleling the trilete rays; these may have a haptotypic origin, and might be equivalent to arcuate ridges in mode of formation.

Spore coat.—Moderately thin (less than 3 microns) and of uniform thickness except at the equator where it is joined by the flange.

Affinities.—Unknown; possibly filicinian. The similarities in morphology suggest that this is a group having natural significance. It may be related to *Granulatisporites*.

Remarks.—The genus is reported from central Russia by Reinsch (1884, his diagnoses 62-66, incl.), from the Ruhr by Loose (1934), and from Lower Pennsylvanian coals of Tennessee by Bentall. Dolgner (1932, pl. 28, fig. 4) has illustrated a form with marginal spines, from Moscow brown coal, which is congeneric with our interpretation of *Reinschospora*; Brokaw has recently found somewhat similar forms in the coal of the Bogota cyclothem (upper McLeansboro age) in the Pennsylvanian of Illinois. The genotype species described below is based on the Tennessee material. The generic name honoring Reinsch seems appropriate inasmuch as Blackburn and Temperley (1936) have shown that the algae formerly known as *Reinschia* probably now

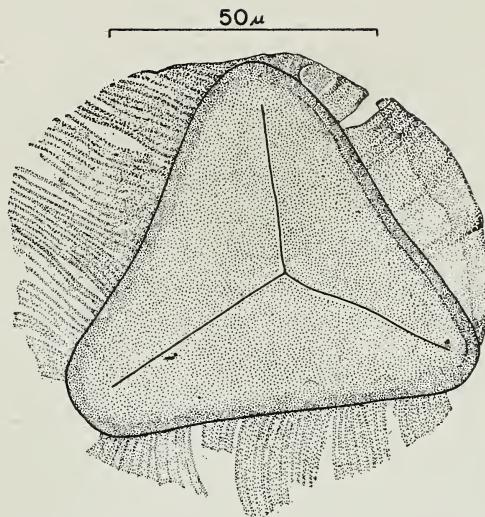


FIG. 2—*Reinschospora bellitas* sp. nov., drawing of holotype.

can be identified with *Botryococcus*. Reinsch's work still is significant and continues to command respect for his voluminous observations.

1. REINSCHOSPORA BELLITAS Bentall, sp. nov. Text figure 2

Description.—Compressed spore subtriangular in outline with inter-radial margins usually concave. Diameters vary from 57 to 76 μ , with an average of about 68 μ . Spore coat less than 2 μ in thickness and levigate. Trilete rays extend four-fifths or more of the distance to the equator. Flange usually originates slightly proximal from the spore equator. Fimbriate elements of flange number about 50 between ray extremities and have a maximum length of 28 μ midway between rays and a minimum length of four to five at the ends of the rays. Incisions of flange, when present, apparently due to imperfect preservation.

Reinschospora bellitas has been isolated from Angel and Battle Creek seams of the southern Tennessee coal field. Though never numerically abundant, it is present in nearly all samples. It is very similar to *R. speciosa* (Loose) but is somewhat larger in size. Occurring with *R. bellitas* is a form essentially comparable in all characters except that the flange is absent. The relationship, if any, between these forms is not known.

Holotype—text figure 2. Tennessee Division of Geology collection; Battle Creek seam, north side of Sweden Cove, Marion County, Tennessee.

2. REINSCHOSPORA SPECIOSA (Loose) S. W. and B., comb. nov.

Alati-sporites speciosus Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 151, pl. 7, fig. 1.

Genus *Lycospora* S. W. and B., gen. nov.

Plate 3, figures 19-19b

Symmetry.—Spores radial; trilete.

Form.—Flattened lenticular as seen in lateral profile, equator marked with a short thick tapering ridge; nearly circular or very broadly triangular in the transverse plane. Compression is generally parallel to the transverse plane with few or no folds, due to preferential orientation of the spores.

Size.—Mean diameter in various species ranging from about 18 to 45 microns.

Ornamentation.—Spores nearly smooth; minutely granulose or rugose. Sometimes the minute rugae tend to be more prominent radially.

Haptotypic features.—Trilete rays extended nearly to margin, suture lines distinct, usually without noteworthy differentiation of lips. In species with most strongly developed emphytic ornament, the haptotypic features also are more prominent. The equatorial ridge corresponds to the arcuate ridge in its origin and rarely becomes so extended and membranous across its width as to resemble a typical flange development. Usually it is narrow and tapers evenly and rapidly away from the spore body; in some species it may be almost nonexistent.

Spore coat.—Relatively thin, sometimes less than 1 micron thick on proximal and distal surfaces and quite translucent. Thicker at the equator where there is no easily defined line of demarcation between the equatorial ridge and the body wall.

Affinity.—Spores of this type have frequently been encountered in the tips of *Lepidostrobus* cones and there is little doubt that most of these forms found isolated represent microspores of the arborescent lepidodendrids. Andrews and Pannell (1942) have described similar forms which persist in tetrad groupings as microspores of a species of *Lepidocarpon*. The microspores of sigillarians (as shown by *Mazocarpon*) are significantly larger and probably are not included in *Lycospora* (cf. Schopf, 1941).

Spores assigned to type D₁ by Raistrick belong without question to *Lycospora*, also probably his B₇ and D₂ Type in part (Raistrick and Simpson, 1933, Raistrick, 1937, 1938). Knox (1938) has recog-

nized the relationship of these types to *Lepidostrobus* and compared D₁ and D₂ with *Lepidostrobus jacksoni* and *L. oldhamius* respectively. Type D₁₁ which she illustrates may also belong to *Lycospora*.

There is, of course, great inherent uncertainty in identifying any species of *Lepidostrobus* from isolated microspores alone. Microfossils of this kind obtainable from coal probably are derived from many more species than are likely to be recognized from entire fructifications because cones are essentially more fragile and require more favorable conditions for their good preservation than spores do. The spores probably constitute a more compete record of the various closely related forms, whether they can be distinguished easily from one another or not.

Reinsch (1884) has illustrated a number of forms, chiefly from central Russia and from Zwickau, Saxony, which are probably referable to *Lycospora*. His numbered diagnoses 32, 81, 83, 87, 240, 424 (?), 525 (?) and 550 may be cited.

Remarks.—Four species previously described are assigned to *Lycospora* all of which represent new name combinations. *Lycospora micropapillata* (Wilson and Coe) is designated as the type species. The genus is well represented in the Pennsylvanian; several additional species have been recognized but are not yet described.

1. LYCOSPORA MICROPAPILLATUS (Wilson and Coe) S. W. and B., comb. nov.
Cirratriradites micropapillatus Wilson and Coe, 1940, Am. Midland Naturalist, vol. 23, no. 1, p. 184, fig. 6.
2. LYCOSPORA MINUTUS (Wilson and Coe) S. W. and B., comb. nov.
Cirratriradites minutus Wilson and Coe, 1940, idem, p. 183, figs. 11 and 12.
3. LYCOSPORA PELLUCIDUS (Wicher) S. W. and B., comb. nov.
Sporites pellucidus Wicher, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 186, pl. 8, fig. 29.
4. LYCOSPORA PUSILLUS (Ibrahim) S. W. and B., comb. nov.

Sporonites pusillus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 448, pl. 15, fig. 20.

Zonales-sporites pusillus (Ibrahim) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 32, pl. 2, fig. 20.

Granulati-sporites pusillus (Ibrahim) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 146, pl. 7, fig. 3.

Genus RAISTRICKIA S. W. and B.,
gen. nov.

Plate 3, figures 18-18b; text figure 3

Symmetry.—Spores radial; trilete.

Shape.—Spherical to slightly flattened in transverse plane and slightly triangular. Little preference as to plane is shown by compressed specimens.

Size.—Spores of different species vary from about 40 to 90 microns in mean diameter.

Ornamentation.—Characteristically verrucose or spinose; spines when present are generally heavy, abruptly truncate, blunt tipped. Close observation often shows the spine tips to be minutely dissected into two to six terminal papillae. The prominences of verrucose forms are similar to the spines but shorter. Except for the trilete structure, features of embrytic ornamentation extend fairly evenly over the whole spore surface.

Haptotypic features.—Trilete rays variable in length as in *Punctati-sporites*; generally inconspicuous, lips unornamented. Rays sometimes slightly undulant due to proximity of spine bases; arcuate distinctions absent.

Spore coat.—Usually of moderate thickness (two to six microns) perisporal membrane lacking.

Affinity.—Typical forms of *Raistrickia* are without doubt filicinae. Spores of *Senftenbergia plumosa*, as identified by Radforth (1938), agree with these of *Raistrickia*, and similar schizaeaceous sporangia obtained by Andrews and Schopf from shale above Illinois coal No. 6 also contain spores of this type. However, the spores of a form identified as *S. pennaeformis* by Radforth (1939) show rather different features, and those of *S. sturi* do not appear congeneric with *Raistrickia*. Although the general relationship cannot easily be doubted, the specific features do not permit easy correlation and *Senftenbergia* and *Raistrickia* no doubt represent generic groups of somewhat different circumscription.

Raistrick's types E₃ and E₄ (Raistrick and Simpson, 1933; Raistrick, 1934, 1935, 1937) belong in *Raistrickia*. His E₃ type is particularly characteristic. That represented as E₄ by Knox (1938), how-

ever, is somewhat questionable. Forms Knox (1938) illustrates as D₃ and D₆ probably belong in this genus. Reinsch (1884) has illustrated only three forms which belong to this group without much doubt. These are described under his diagnoses 52, 308, and 588 from central Russia and from Zwickau, Saxony. The form illustrated by Thiessen (1920) in plate 61, figure B, from Benton, Illinois (probably the Herrin No. 6 coal), is characteristic of *Raistrickia*; that shown above it in horizontal thin section may likewise belong here but it is impossible to be sure. The two illustrations show the inadequacies of thin sections for identification of spores.

Remarks.—Five species previously described are assigned to *Raistrickia*. These forms are widely distributed as may be inferred from the preceding discussion. None of these previously named are very suitable for designation as a type, however, inasmuch as the more typical form, which particularly seems generically distinct from *Punctati-sporites*, has not previously been formally designated although it seems fairly common. Furthermore, inadequacies in the previous descriptions and illustrations also militate against selection of any of them as types for this genus. The species described below, *Raistrickia grovensis* sp. nov. is therefore designated as the type.

1. RAISTRICKIA (?) ABDITUS (Loose) S. W. and B., comb. nov.
Sporonites abditus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 451, pl. 19, fig. 53.
Verrucosi-sporites abditus (Loose) Loose 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 154.
2. RAISTRICKIA FIBRATUS (Loose) S. W. and B., comb. nov.
Sporonites fibratus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 451, pl. 19, fig. 52.
Setosi-sporites fibratus (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 148.
3. RAISTRICKIA GROVENSIS Schopf, sp. nov.
Text figure 3

Description.—Spore rounded triangular in outline, about 50 microns in diameter. Ornamented with numerous short (3-5 μ) broad (2-6 μ) blunt tipped spines, which by juxtaposition sometimes appear to be mutually attached. Rays 15-20 μ long, slightly undulating, lips not raised but forming a narrow margin on either side of the suture line. Wall somewhat vari-

able (3-4 μ) in thickness, appearing brownish translucent; spines are darker.

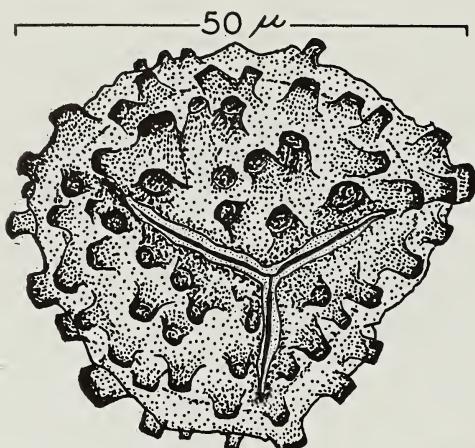


FIG. 3—*Raistrickia grovensis* sp. nov., camera lucida drawing of holotype.

This form, in general, resembles the spores of Radforth's (1938) *Senftenbergia plumosa* but the spines are shorter, broader and less crowded and the spores he illustrates are round in outline. It is difficult to make a precise comparison with other previously described species now assigned to *Raistrickia* because of inadequacies of their description and illustration. The spine tips of this form are entire and rounded; others from the same coal bed and elsewhere show spine tips slightly dissected. No doubt several species of schizaeaceous ferns are represented. The specimen shown in text figure 3 designated as holotype, is from the Herrin (No. 6) coal (uppermost Carboniferous age) which is worked by extensive open-cut mining operations near Middle Grove, Illinois, in northern Fulton County.

4. *RAISTRICKIA SAETOSUS* (Loose) S. W. and B., comb. nov.

Sporonites saetosus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt., B., p. 452, pl. 19, fig. 56.

Setosi-sporites saetosus (Loose) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 26.

Setosi-sporites saetosus (Loose) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 148.

5. *RAISTRICKIA SPINOSAETOSUS* (Loose) S. W. and B., comb. nov.

Sporonites spinososaetosus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 452, pl. 19, fig. 55.

Apiculati-sporites spinososaetosus (Loose) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 24.

Apiculati-sporites spinososaetosus (Loose) Ibrahim, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 153.

6. *RAISTRICKIA SUPERBUS* (Ibrahim) S. W. and B., comb. nov.

Setosi-sporites superbus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 27, pl. 5, fig. 42.

Genus *FLORINITES* S. W. and B., gen. nov.

Plate 2, figures 13-13b; text figures 4, 5

Symmetry.—Pollen grains apparently bilateral; they may nevertheless be derived from tetrahedral tetrads.

Form.—Broadly elliptical in outline due to the form of the bladder; body somewhat more spherical and nearly entirely enclosed by the bladder; greatest diameter of body corresponds to the major diameter of the bladder. When compressed the bladder oftentimes is least affected by folding; the body generally is marked by numerous sharp angular folds, especially around its periphery.

Size.—Greatest diameter (length of bladder) among different species varies from about 50 to 180 microns; the pollen body proper varies from about 20 to 110 microns in diameter in individuals of various species.

Ornamentation.—Bladder ornament similar to that of *Endosporites* and *Pityosporites*; exterior surface smooth or very finely granulose or rugose, internally the membrane bears a distinct reticulation net which tends to be obsolescent in the central proximal area. Bladder and body walls are joined distally, and centrally from this juncture there is no evidence of reticulation.

Haptotypic features.—Generally not evident, and probably always extremely obscure. Trilete imprint (when discernible) is wholly vestigial, probably located entirely on the bladder, and has no functional significance in the mature spore. The effect of the haptotypic relations sometimes may be obscurely expressed in the proximal bladder reticulation pattern.

Spore coat.—Bladder membrane is expanded on all sides of the body except for a small distal area. The bladder membrane generally has a very well defined reticulation network located on the inner surface. At the folded margin the bladder membrane commonly appears thicker than it actually is due to the reticule bars appearing in profile; the membrane proper usually is less than a micron thick. Consequently, it is highly translucent between

the bars of the reticulum which may be extended as much as 2 or 3 microns away from the membrane surface. The body wall inside the bladder is everywhere thin, oftentimes less than a micron, and shows no structural differentiation. Because of its tenuousness, it may not be exosporal in nature although it would seem rather precisely equivalent to the thicker and presumably exosporal body wall of *Endosporites*. The body wall of *Florinites* is slightly less translucent than the bladder due in considerable part, at least, to its rather numerous folds.

Affinity.—*Florinites* is known to be related to *Cordaianthus* (pars), *Lebachia*, *Ernestiodendron* and *Walchianthus* through the investigations of Florin (1936, 1938-40); thus it seems evident that it represents a part of the upper Paleozoic gymnospermic alliance.

That some cordaitaleans possess pollen grains of the *Endosporites* type is shown by *Cordaianthus* cf. *C. shuleri* Darrah represented in collections made by Wilson. Similar pollen grains are shown by Oliver (1940) to be present in the pollen chamber of "*Stephanospermum*" *caryoides* which, according to Florin (1937, p. 310), is no doubt a cordaitalean seed. Oliver's figures 40 and 42 show a characteristic, and no doubt functional, trilete apparatus. Florin's study of *Cordaianthus saportanus* pollen and pollen grains of *Florinites* type associated with it (his *Cordaianthus* sp. 1 and 2) indicates that the suture was entirely absent and the trilete marking completely vestigial. In the walchian conifers not even a vestigial remnant of the haptotypic marking has been reported but it might be present (just as in the *Cordaianthus* sp. 2) and still not be easily demonstrable from coalified compression material. The agreement in pollen structure between the *Cordaianthus* material studied by Florin, and his walchians is such as to leave little doubt that a direct relationship exists between them. Just how this relation evolved and should be systematically expressed cannot now be stated. The pollen structure is so specialized, particularly when compared with the expression of spore characteristics elsewhere in the plant kingdom, as to permit no conclusion other than direct relationship. The possibility of convergent evolution being responsible for the struc-

tural similarity in the two instances is entirely remote.

These gymnospermic groups, often-times regarded as distinct, thus have a community of relationship which is meagerly expressed for the present in the genus *Florinites*. The probability is that this group will also be of continuing value for classification of these spores. If plants of the cordaito-coniferous type were partially restricted to upland habitats their pollen grains may offer the only widespread available record of their existence. For this reason it is essential that they be classified as precisely as possible.

Florinites is also related to *Endosporites*, *Pityosporites*, *Alisporites*, and *Parasporites*, all of which have the characteristic bladder-forming perisporal (?) membrane. The study of these in conjunction with fructifications and other organs with which they are more or less definitely correlated cannot fail to add greatly to our knowledge of gymnospermic phylogeny during a critical period in the evolution of this plant group. The definition of the age at which these genera are first recognizable will be of geologic as well as botanical significance.

Remarks.—This genus is proposed to apply to gymnospermic plants whose pollen generically corresponds with the type species as expressed, in general, by the foregoing definition. Florin has given rather similar data in description of the species "*cordaitiformis*" which he places under the genus name *Pollenites* (see below). There is little doubt that such a generic designation is inadequate but question may arise concerning the validity of the specific epithet.

Pollenites cordaitiformis was established to include pollen which elsewhere in his monograph Florin had assigned to five other species of plants. The only illustrations given to validate the name had also previously been allocated differently to the other five species. Florin's photographs still serve as an excellent basis for discussion of the character of isolated *Florinites* pollen but none of those he illustrated are properly identified with this genus because no single organism can have more than one valid name. Specimens properly assigned to *Lebachia*,

Ernestiodendron, or *Walchianthus* cannot in the same instance also be assigned to some different genus and species. Furthermore, it seems an absurdity to attempt to make an identification with a generalized group such as *Pollenites* or even *Florinites*, when a more precise specific pertinence is thoroughly demonstrated. The systematic problem that confronts us revolves around proper determination of fossils where pertinence to a definitely restricted group is, for one reason or another, legitimately in question. Thus it would seem that unless one of the pollen specimens Florin has illustrated is regarded as improperly referred to species of *Lebachia*, *Ernestiodendron*, or *Walchianthus*, none of them can be regarded as type material of a new distinct taxonomic species. As there is no discernible reason to question Florin's more precise assignment of that material, it seems equally evident that *Pollenites cordaitiformis* has no type and the name was superfluous as proposed.

Florinites antiquus sp. nov. is described below and designated as the type species. Two other species previously described also are tentatively assigned to the genus. There can be little doubt that Types 5 of Millott (1939) and 3K of Knox (1942) are also congeneric. Florin's various descriptions and excellent illustrations have shown clearly that a number of other species can be distinguished by their pollen characters.

Florinites is known to be widely distributed in the Pennsylvanian and Upper Carboniferous as well as in the Permian strata where other coniferous remains are associated with it. Pollen of this character has been found to be abundant in some Tennessee coals and other beds of lower Pottsville age. It seems likely that a detailed study of these forms will add much to our knowledge of the early ancestry of conifers.

1. FLORINITES ANTIQUUS Schopf, sp. nov.

Text figures 4, 5

Description.—Pollen grains, bilateral symmetry, equipped with an annulate bladder joined to the central pollen body only on the distal side, thus outlining a "contact area" equivalent to a germinal "furrow." The grains are broadly elliptical when compressed in the proximo-distal plane so that the length and breadth proportions

are evident. When compressed laterally the axial dimension is observed to be shorter than that in either of the other two planes of symmetry. Inclusive of the bladder, the fossils range from 55-90 (mostly 65-85) microns in length, and 40-75 (mostly 45-60) microns in breadth. The axial dimension, exhibited in a few instances, is a little less than 40 microns. The body, enclosed by the bladder on all but the distal side, is more nearly spherical ranging from 25-45 (mostly 27-37) microns in length and 20-40 (mostly 25-35) microns in breadth. The axial dimension of the body is somewhat less, about 20-25 microns. The body proper is always compressed with sharp folds which are characteristically more numerous around the periphery; the bladder is oftentimes hardly folded when compression is in the proximo-distal plane, but the folding that does affect it is more erratic. When compressed obliquely or laterally the outline is much distorted. The bladder membrane itself is less than a micron thick; a zone a few microns broad around the equator is more definitely yellowish translucent and slightly thicker; compressed laterally the equatorial zone of the bladder remains distinguishable and the slight inequality in thickness evidently contributes to the more erratic character of folds. The bladder is smooth to minutely granulose externally but shows an internal reticulation net. The reticulae vary from 1 to 3 microns in diameter and may be very slightly elongated radially. The bars of the reticulation are not prominent in this species and have a thickness of a fraction of a micron. The reticulation is more pronounced away from the body and is hardly discernable immediately surrounding the "contact area" on the distal side or centrally on the proximal side. The body wall is essentially smooth, very thin, and except where folded into several thicknesses, it hardly darkens the light straw-yellow translucence of the central area of the pollen grain. The "contact area" where bladder joins the body wall is elliptical or oval with its greater diameter commonly transverse to the length of the pollen grain. The margins of this area are quite faint and its size and outline vary from 17 x 23 to 10 x 20 microns. It can hardly be detected under the microscope unless the grain is oriented distal side up. A distinct but tenuous striation traverses the "contact area" in many instances, continues on the bladder membrane until about opposite the body margin, and is then lost as the bladder membrane develops its more distinctive ornamentation. It can hardly be interpreted as a monolet suture line; it would seem more plausibly regarded as a harmomeric groove similar in character to those on the distal side of *Monoletes* prepollen but more faintly developed, since the body and bladder membranes are not nearly so thick as the *Monoletes* coat. The striation seems correlated in position with the long axis of the contact area and frequently is set obliquely with reference to the breadth of the grain as a whole.

Haptotypic characteristics are very faint and may be observed to best advantage in forms in which the body membrane is wanting, but the bladder membrane persists (perhaps as a result of maceration). In such examples, which are

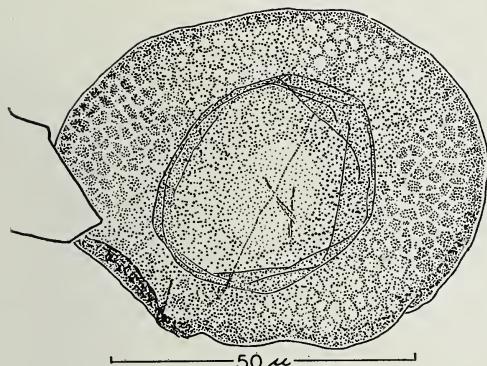


FIG. 4—*Florinites antiquus* sp. nov., drawing from microprojection of holotype.

fairly common, there is a central gap or tear in the bladder membrane on the distal side corresponding to the "contact area" and the central proximal region of the bladder wall is visible without any overlying layers. Granules seem aligned in a semblance of a central trilete pattern, obsolescent, with rays perhaps 6 microns long; the granulation of the surrounding area of the bladder membrane (it is too faint to be recognizable as reticulation) also seems faintly aligned to correspond to three radii. Conclusive definition is difficult in material obtained by coal maceration but such specimens tend to confirm Florin's (1936, p. 637) interpretation of proximal structure in the more highly reticulate and better preserved pollen identified by him as *Cordaianthus* sp. 2.

Florinites antiquus seems distinguishable from all the similar forms Florin (1936, 1938-40) has identified with *Cordaianthus*, *Lebachia*, *Ernestiodendron*, and *Walchianthus*, on the basis of its size. *F. antiquus* is evidently significantly smaller judging from measurements Florin has given and by dimensions measured directly from the illustrations he has published. His *Cordaianthus* sp. 1, from the Stephanian of France compares most closely in size, (bladder length, 78-90; width, 62-67 microns; body length, 42-50; width 40-48 microns). The differences can best be evaluated by reference to the assembled measurements of *F. antiquus* presented in text figure 5. Presumably the flattening of *F. antiquus* pollen grains would give rise to dimensions which are slightly excessive in the plane of compression and therefore not quite comparable to measurements taken from Florin's uncompressed forms. That the species are distinct is evident from the much less pronounced bladder reticulation in *F. antiquus*. The distal striation has not been noted in forms regarded as cordaitean but is evident (though no mention is made of it) in several of Florin's figures of Paleozoic coniferous pollen. (cf. Florin, 1939, pls. 55-56, fig. 21; Florin, 1940, pls. 145-146, fig. 19; ibid, pls. 147-148, fig. 5).

From its age (early Allegheny) one might assume that *F. antiquus* belonged with the cordaitealeans, but its features are advanced on

a par with that of the Paleozoic Coniferales. When the conifers first made their appearance in the Missouri series in Kansas, they already were highly developed plants whose previous ancestry must have been of some considerable duration. Thus it seems equally plausible that these pollen grains of advanced character and older derivation may actually be coniferous. The pollen grains, it must be recalled, are the most widely distributed of the determinable fossil plant entities and the pollen membranes are among the most indestructible in fossilization of any known plant materials. It is to this fossil-pollen record that one would most logically turn to obtain earliest evidences of newly differentiating plant groups that became established among the upland vegetation of the period.

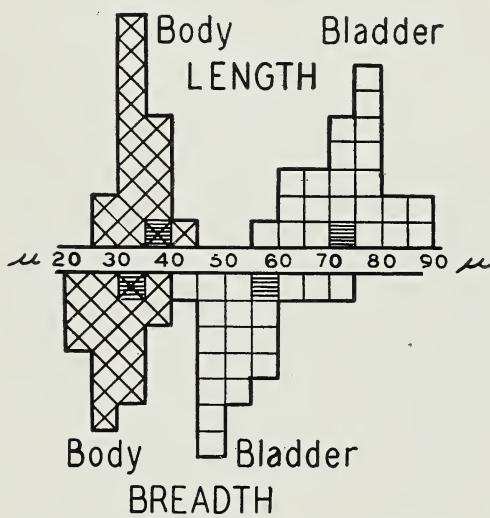


FIG. 5—*Florinites antiquus*, coordination of length-breadth measurements from 23 specimens, grouped according to 5 micron increments. (Dimensions modified by unusual folding have been omitted). Cross-lined areas represent measurements from the holotype.

F. antiquus has been obtained in moderate abundance from a widespread 10 to 12-inch coal in the Wiley cyclothem where it crops out along Soap Creek southeast of the town of Carbon, Davis County, Iowa. Correlation with the widespread Wiley coal of western Illinois has recently been confirmed by L. M. Cline of Iowa State College, who has measured the section, showing this coal to be in proper sequence and about 12 feet above the lower Seahorne coal and limestone developed in this area. The Wiley cyclothem is near the top of the Tradewater group of Illinois and is considered to be lower Allegheny in age.

The holotype of *F. antiquus*, illustrated in text figure 4, is from maceration 413, slide 8 (unstained) in the Illinois State Geological Survey collections in Urbana.

2. FLORINITES (?) PUMICOSUS (Ibrahim) S. W. and B., comb. nov.

PALEOZOIC FOSSIL SPORES

Sporonites pumicosus Ibrahim, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 447, pl. 14, fig. 6.

Reticulata-sporites pumicosus (Ibrahim, 1932) Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 38.

Reticulata-sporites pumicosus (Ibrahim, 1932) Ibrahim, 1933, Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 157, pl. 7, fig. 29.

3. FLORINITES (?) VISENDUS (Ibrahim) S. W. and B., comb. nov.

Reticulata-sporites visendus Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 39, pl. 8, fig. 66.

INCERTAE SEDIS

In the present state of knowledge there are a number of named forms which it is impossible to treat systematically. The various generic designations listed below may possibly have a certain value but in any event their significance does not appear to be biological. The names *Sporites* (H. Potonie, 1893), *Pollenites*, and *Sporonites* (R. Potonie, 1931) cannot be regarded as having systematic value. Forms listed in these groups have no essential biologic features in common, no type species are recognized, and no systematic treatment is feasible on this basis. A morphologic designation apparently would have served as well to record the lack of systematic information concerning most material of this character. It likewise seems impossible to attach any generic significance to the names *Verrucosa-sporites* (Loose, 1934), *Elongatosporites* (Berry, 1937), *Punctata-sporites* or *Zonala-sporites* (Ibrahim, 1933). Such problematic forms as have been listed under these names must await future disposition.

1. SPORITES ECHINOSPINOSUS Zerndt, 1937, Acad. polonaise sci. Trav. Geol. no. 3, Krakow, p. 17, pl. 24, figs. 5-10.
2. SPORITES FUMOSUS Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, p. 52, pl. 5, figs. 1-2.

3. SPORITES HIRMERI Reissinger, 1939, Paleontographica, vol. 84, Abt. B, p. 16.

Note.—Nomen nudem, no illustration.

4. SPORITES IRREGULARIS Reissinger, 1939, Paleontographica, vol. 84, Abt. B, p. 17.

Note.—Nomen nudum, no illustration.

5. SPORITES PLICATUS Schopf, 1938, Illinois Geol. Survey Rept. Inv. 50, p. 51, pl. 7, figs. 7-9.

6. SPORITES PROBLEMATICUS Zerndt, 1934, Acad. polonaise sci. Trav. Geol. no. 3, Krakow, p. 27, fig. 13, pl. 30, figs. 1-10.

7. SPORITES SPONGIFORMIS Reissinger, 1939, Paleontographica, vol. 84, Abt. B, p. 17.

Note.—Nomen nudum, no illustration.

8. SPORONITES BIPOROUS Berry, 1937, Am. Midland Naturalist, vol. 18, no. 1, p. 160, fig. 14.

9. SPORONITES TRIPTERUS Berry, 1937, Am. Midland Naturalist, vol. 18, no. 1, p. 160, fig. 8.

10. ZONALA-SPORITES TACITURNUS (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 157.

Sporonites taciturnus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 450, pl. 18, fig. 38.

11. ZONALA-SPORITES ULUGBEKI (Loose), Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 38, pl. 1, fig. 11.

Sporonites ulugbeki Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B, p. 447, pl. 14, fig. 11.

12. ELONGATO-SPORITES RETICULATUS Berry, 1937, Am. Midland Naturalist, vol. 18, no. 1, pp. 158, 160, fig. 12.

13. VERRUCOSA-SPORITES PERVERRUCOSUS (Loose) Loose, 1934, Inst. Paläobot. Arb., vol. 4, no. 3, p. 157.

Sporonites perverrucosus Loose, 1932, Neues Jahrb., Beilage-Band 67, Abt. B., p. 451, pl. 18, fig. 48.

14. PUNCTATA-SPORITES SABULOSUS Ibrahim, 1933, Sporenformen des Aegirhorizonts, p. 37, pl. 5, fig. 43.

In addition, the following types of Raistrick and Knox may be listed, for they too are of uncertain affinity at the present time. Some of these seem to be worthy of more appropriate classification. Raistrick (1937, p. 911) B₂, B₄, E₂, E₆, G₁, Knox (1942, pp. 100-101), D₅, K₈.

SUMMARY

This report presents the revised classification of plants identified from their isolated fossil spore coats, and deals primarily with those of Paleozoic age. Orthodox taxonomic procedure has been followed as closely as possible for reasons which are presented in the introduction. A cautious policy has been followed with regard to synonymy, and, even though forms are very closely allied, names based on different holotypes have been allowed to stand. In many instances, however, the apparent close relationship, which may later prove conspecific, has been noted. Thus names noted as synonyms are nearly all objective synonyms because they are based on a common holotype. Many difficult problems concerning nomenclature of fossil plants are solvable if nomenclatural types are strictly interpreted.

About 400 named species have been included in the present paper and most of these have been allocated among 23 genera which seem to serve a useful and significant purpose in classification. Additional genera no doubt will require recognition later and new information will modify the views that have been expressed for the genera described here. A number of species described previously apparently do not conform sufficiently to merit inclusion in the same genus with the type species of the group, and at the same time do not show convincing evidence of affinity with other recognized groups. Such forms have been listed as *species excludende*. Attention is directed to the several species excluded from *Reticulatisporites* which here is interpreted in a considerably restricted sense. Many of these forms require much more careful study in order to arrive at a satisfactory expression of their affinity and classification. Other forms listed under *incertae sedis* also are lacking in sufficiently understood biological characteristics to support a definite systematic allocation. In dealing with plant micro-

fossils it seems unavoidable that many forms worthy of description will nevertheless have such problematical relationship that their assignment under *incertae sedis* is obligatory. The usefulness of fossils nevertheless bears a considerable relationship to the basic and fundamental information available about them and for this reason greatest significance must be attached to species whose relationship has been reliably established.

The authors of this paper and their associates have observed many new types of plant microfossils in preparations from coal and carbonaceous sediments in America. The present synopsis is the outgrowth of a need for a more comprehensive survey of previous work considered from the standpoint of a consistent systematic policy. The essential features of an appropriate policy have been embodied here to serve as a working basis for the great amount of descriptive work yet to be done. We believe that this working basis will require further revision as new information is accumulated and presented. We further believe that such revision can be carried out with greatest efficiency and benefit to all concerned if the orthodox usages characteristic of mature systematic science are adopted and critically applied.

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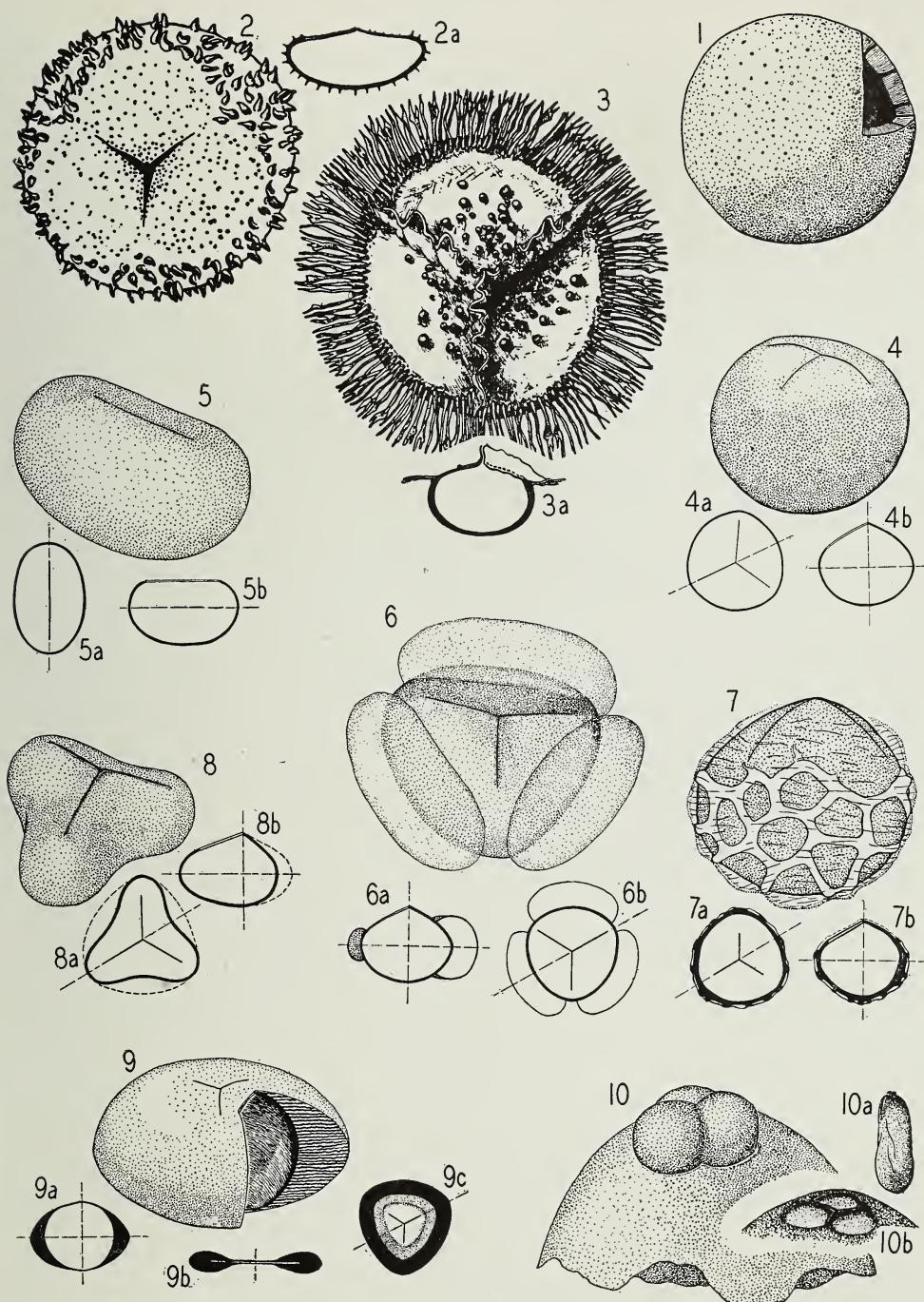
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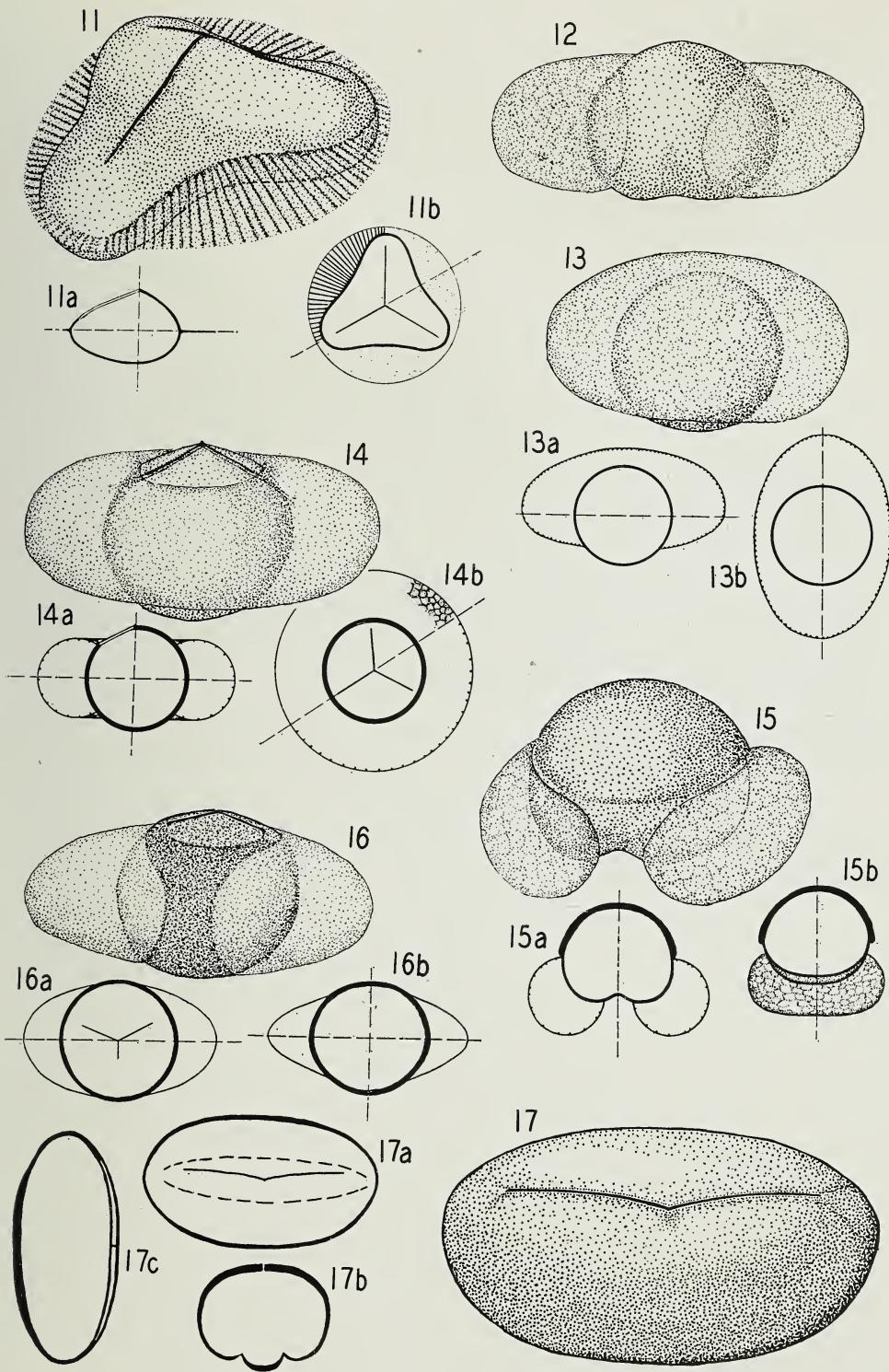
EXPLANATION OF PLATE 1

- FIG. 1—*Tasmanites*; segment cut away to show mode of perforation. Symmetry is unicentric with no axis more developed than another p. 11
- 2—*Triletes*; specimen of the sectio *Aphanozonati*; after Zerndt; 2a, diagram showing uncompacted form in the axial plane corresponding with a trilete ray p. 18
- 3—*Triletes radiosus*; sectio undifferentiated; after Zerndt; 3a, diagram showing uncompacted form in the axial plane corresponding with a trilete ray pp. 18, 24
- 4—*Punctati-sporites*; 4a, equatorial (transverse) plan; 4b, axial (longitudinal) plan . . p. 29
- 5—*Laevigato-sporites*; 5a, equatorial (transverse) plan; 5b, longitudinal plan corresponding with the longest axis p. 36
- 6—*Alati-sporites*; 6a, axial (longitudinal) plan; 6b, equatorial (transverse) plan . . p. 33
- 7—*Reticulati-sporites*; in some instances the reticulation may cover proximal and distal hemispheres about equally; 7a, equatorial (transverse) plan; 7b, axial (longitudinal) plan p. 34
- 8—*Granulati-sporites*; 8a, equatorial (transverse) plan; 8b, axial (longitudinal) plan . p. 32
- 9—*Denso-sporites*; segment cut away to show thickening of peripheral region of spore coat; 9a, axial (longitudinal) plan uncompacted; 9b, form such spores habitually assume under normal compression; 9c, equatorial (transverse) plan p. 39
- 10—*Cystosporites*; proximal end of spore with three abortive tetrad members attached at the apex; 10a, small drawing of complete fertile spore; 10b, apex of fertile spore showing trilete apparatus when abortive members are disconnected p. 40



EXPLANATION OF PLATE 2

- FIG. 11—*Reinschospora*; 11a, axial (longitudinal) plan; 11b, equatorial (transverse) plan . . p. 52
- 12—*Alisporites*; axial (longitudinal) plan not shown; much the same as 16b but body wall thinner p. 48
- 13—*Florinites*; 13a, axial (longitudinal) plan, proximal side up; 13b, equatorial (transverse) plan. The body tends to be slightly elliptical, the long dimension agreeing with that of the bladder p. 56
- 14—*Endosporites*; 14a, axial (longitudinal) plan; it is difficult to judge whether the bladder and body wall always join distally as shown here; 14b, equatorial (transverse) plan p. 44
- 15—*Pityosporites*; pollen grains of modern aspect; 15a, axial (longitudinal) plan in the plane corresponding with the sulcus between the bladders; 15b, axial (longitudinal) plan in the plane of the bladders p. 27
- 16—*Parasporites*; 16a, equatorial (transverse) plan; 16b, axial (longitudinal) plan . . p. 42
- 17—*Monoletes*; 17a, equatorial (transverse) plan; 17b, axial plan view corresponding to the short dimension, distal grooves down, proximal suture up; 17c, axial plan view corresponding to the long dimension p. 38

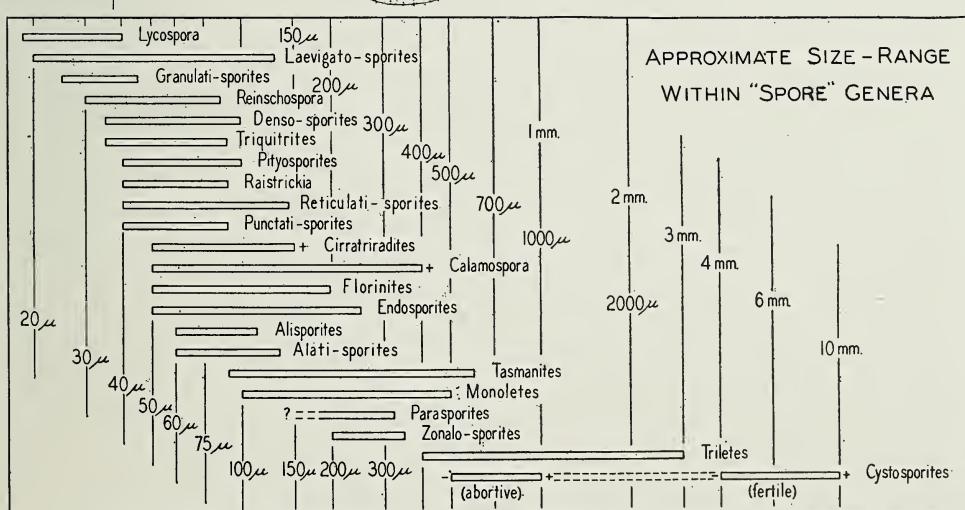
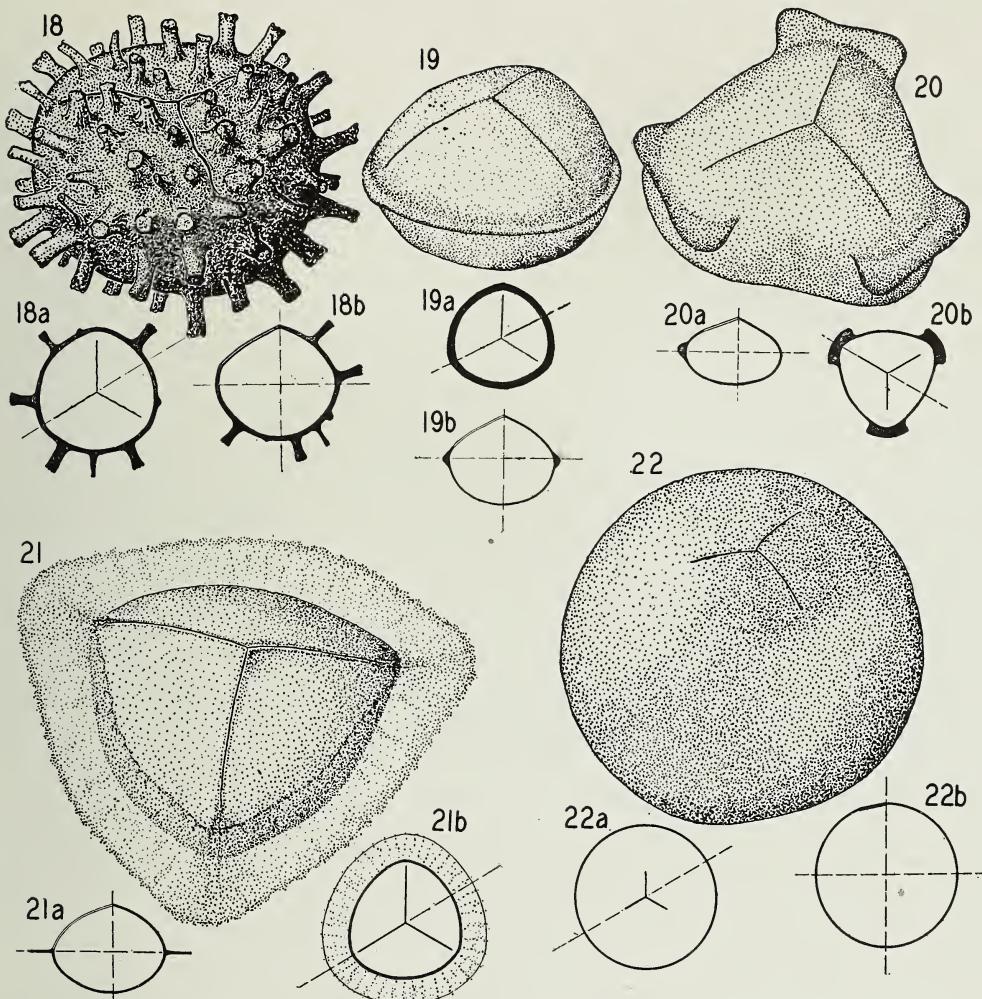


EXPLANATION OF PLATE 3

- FIG. 18—*Raistrickia*; 18a, equatorial (transverse) plan; 18b, axial (longitudinal) plan . . . p. 55
19—*Lycospora*; 19a, equatorial (transverse) plan; 19b, axial (longitudinal) plan . . . p. 54
20—*Triquitrites*; 20a, axial (longitudinal) plan; 20b, equatorial (transverse) plan . . . p. 46
21—*Cirratiradites*; 21a, axial (longitudinal) plan; 21b, equatorial (transverse) plan . . p. 43
22—*Calamospora*; 22a, equatorial (transverse) plan; 22b, axial (longitudinal) plan . . . p. 49
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(Below)

Graphic comparison of approximate size range of fossils included in the various genera. Dimensions are indicated in logarithmic coordination.



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